COMPETITION AMONG FOUR SPECIES OF HYMENOPTEROUS PARASITOIDS OF THE CARIBBEAN FRUIT FLY, *Anastrepha suspensa* (LOEW)

BY

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To

the late Mr. R.W. Swanson

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Three solitary larval-pupal parasitoid species, Biosteres longicaudatus Ashmead, Opius concolor Szep., and Trybliographa daci Weld, and the solitary pupal parasitoid Dirhinus giffardii Silv. have been introduced into Florida for the biocontrol program against the Caribbean fruit fly, Anastrepha suspensa (Loew). One of the four, B. longicaudatus, has been established in the field.

The biological characteristics of each species and the intra- and interspecific relationships among the four species were studied. Besides parasitism, O. concolor killed 20.96% of the hosts by causing ring-structure injury around the postcephalic 4th and 5th segmental areas of the pupa. Eggs and 1st instar larvae of T. daci were often found to be encapsulated. Data indicating cleptoparasitic behavior of T. daci are statistically significant at the 0.05 level. Cleptoparasitic behavior

would appear to be a selectively advantageous behavioral response to the host's ability to resist parasitism through encapsulation.

T. daci preferred to oviposit in the postcephalic 3rd and 4th segmental areas, while D. giffardii perferred the caudal segmental areas. Egg distribution of B. longicaudatus, T. daci, and D. giffardii in hosts was nonrandom, and that of O. concolor random. All four of the species showed host discrimination ability. T. daci preferred hosts already parasitized by either B. longicaudatus or O. concolor. D. giffardii showed better oviposition restraint ability than other species when the parasitoid to host ratio was high.

Supernumerary progeny were eliminated by intra- or interspecific cannibalism in B. longicaudatus, O. concolor, and T. daci. In D. giffardii, cannibalism was used only to eliminate its own species. In interspecific competition D. giffardii eliminated its competitors by means of physiological suppression.

Total host mortality was positively related to host density, and the relation became stronger as parasitoid density increased. Searching efficiency of individual parasitoids diminished with increased parasitoid density as a result of mutual interference among searching adults, and the percentage of searching time increased as parasitoid density increased.

Parasitoid sex ratio was altered by the degree of intraspecific competition intensity. Based on the combined biological characteristics, competitive ability, and reproductive capacity, B. longicaudatus was the superior species, followed by D. giffardii, T. daci, and O. concolor.

CHAPTER I
INTRODUCTION

The utility of single vs. multi-species parasitoid introduction has been a major controversy in classical biological control. Turnbull and Chant (1961) suggested that no multi-importation should be made, believing the competition between species would reduce the effectiveness of a particular species (Turnbull and Chant 1961, Watt 1965, Force 1974, Ables and Shepard 1976, Pschorn-Walcher 1977). In contrast, Silvestri (1932) argued that differences in the morphological and physiological characteristics of several control agents would increase the likelihood that at least one introduced species would adjust to short term or localized variations in the new environment (Smith 1937, Doutt and DeBach 1964). Other authors have concurred that interspecific competition may reduce the control efficiency of individual species when multi-species parasitoid introduction is attempted. Nevertheless, some researchers found the total mortality to the host population to be greater when using several species rather than a single control agent (Smith 1929; Huffaker et al. 1971; Ehler 1977, 1978, 1979; Miller 1977; Propp and Morgan 1983; Browning and Oatman 1984).

Prior to any introduction of control agents, it is desirable to have an understanding of (1) the biology of each species; (2) the relationship between each species and its host; and (3) the relationship between each species and competing species. The information obtained about each

of these is important in making a rational and effective selection of the released species.

In order to be efficient in finding and utilizing their host insects, parasitoids are dependent upon certain basic biological, morphological, physiological, and reproductive characteristics. Not all the characteristics of each species may meet DeBach's (1974) criteria for "best" parasitoid, but the diverse characteristics of different parasitoids provide unique opportunities for competition and/or survival. Those diverse characteristics are termed "adaptive strategies" by Force (1972) and Price (1973a,b 1975). The interrelationships between host and parasitoid have been grouped into three major processes: (1) host selection (Vinson 1976); (2) host suitability (Vinson and Iwantsch 1980a); and (3) host regulation (Vinson and Iwantsch 1980b). Knowledge of each of these processes will be helpful in predicting the prospects for survival and establishment of a species under consideration for introduction. Finally, competition is a major interaction within or among parasitoid species, and may influence survival of individuals and negatively affect persistence of populations.

Four hymenopterous species were utilized in this study. They included three species, Biosteres longicaudatus Ashmead, Opius concolor Szep. and Trybliographa daci Weld, that attack larvae, and one species, Dirhinus giffardii Silv., that attacks pupae. They were imported into Florida for the biological control of the Caribbean fruit fly, Anastrepha suspensa (Loew). Only B. longicaudatus is known to be established in the field. The objectives of this research were to (1) review some basic morphological, biological, physiological, behavioral and reproductive characteristics of each species; (2) study the ability of each species in

regard to host discrimination and oviposition restraint; (3) examine intraspecific and interspecific competition and their resultant impact on host mortality and parasitoid sex ratio; (4) evaluate the effectiveness of single and multi-species release based on the interactions of the four parasitoid species studied and their relationship with the host; and (5) based on results of the above studies, pragmatically determine first, whether additional species should be released and, secondly, in the event additional releases are indicated to recommend which of the three species would be most useful.

CHAPTER II
LITERATURE REVIEW

Host and Interacting Parasitoid Species

Anastrepha suspensa (Loew)

Systematics. A. suspensa belongs to the family Tephritidae and the order Diptera. The genus contains 155 species (Steyskal 1977) of which 16 have been identified in the United States. Six of those are found in Florida (Rohani 1980).

A. suspensa was described by Loew in 1862 from specimens collected in Cuba (Greene 1934). Synonyms of A. suspensa are

Trypeta suspensa Loew, 1862

(Trypeta) Acrotoxa suspensa (Loew), 1873

Anastrepha unipuncta Sein, 1933

Anastrepha longimaculata Greene, 1934

Distribution. A. suspensa is known from Cuba, Jamaica, Hispaniola, Puerto Rico, and Florida (Weems 1965). In Florida, A. suspensa was first identified through adults collected at Key West in 1931. No specimens were collected from 1936 until 1959 when two adults were found at Key West. A. suspensa was rediscovered in Miami Springs in 1965, and has since spread into 34 counties, the most northern boundaries of infestation being Duval, St. Johns, Putnam, Marion, and Citrus Counties (Weems 1965, 1966; Anonymous 1967, 1969, 1971, 1979).

Hosts. Weems (1965) identified the known field hosts of A. suspensa in Greater Antilles. The preferred species were Psidium guajava L., Syzygium jambos (L.) Alst. and Terminalia catappa L.

Swanson and Baranowski (1972) reported fruits of 84 plant species in 23 families served as hosts for A. suspensa in Florida. Preferred species were found to be Eriobotrya japonica (Thunb.) Lindl., Eugenia uniflora L., Psidium cattleianum Sabine, P. guajava L., Syzygium jambos (L.) Alst. and Terminalia catappa L. Eleven species or cultivars of citrus are among the 84 known hosts. Most of the citrus attacked were backyard fruits in overripe condition and the infestation was low (Swanson and Baranowski 1972). However, the fact that A. suspensa was found to develop in citrus was reason to fear that the species would prove to be a serious pest of the important crop.

Natural enemies. Several parasitoids have been reported from or released against A. suspensa (Table 1). Among those released, Biosteres longicaudatus Ashmead, Doryctobracon (=Parachasma) cereum (Gahan) and Opius anastrephae Vier have been established in the field (Baranowski and Swanson 1971, Swanson 1979). Two predators, Fulvius imbecilis (Say) (Hemiptera: Miridae) and Xylocoris galactinus (Fieb.) (Hemiptera: Anthocoridae) are known to prey on A. suspensa (Baranowski and Swanson 1971). A fungus, Entomophthora dipterigina (Thaxter), has also been reported to cause adult mortality (Swanson 1971).

Biology. A. suspensa mass rearing techniques were studied by Burditt et al. (1975), who used a corncob based larval diet while Baranowski (Greany et al. 1976) developed a sugarcane bagasse diet. The optimum temperature for mass rearing was between 25°C to 30°C (Prescott and Baranowski 1971). There are three instars each with characteristic mouth hooks, and development from egg to adult requires 19-21 days at 27.5°C (Lawrence 1975, 1979). The reproductive systems of adults were described by Dodson (1978). By means of laboratory bioassay Nation (1972)

Table 1. The introduced and native hymenopterous parasitoids found to attack A. suspensa (Loew).

Parasitoid	Stage attacked	Location	Source	Reference
Braconidae				
Biosteres longicaudatus (Ashmead)	larva	Florida	Hawaii	Swanson 1971
Biosteres oophilus (Fullaway)	larva	Florida	Hawaii	Swanson 1977
Biosteres tryoni Cam.	larva	Puerto Rico	Hawaii	Bartlett 1941
Dorycotobracon cereum (Gahan)	larva	Puerto Rico	Brazil	Bartlett 1941
		Florida	Trinidad	Baranowski & Swanson 1971
Doryctobracon trinidadensis (Gahan)	larva	Florida	Trinidad	Swanson 1979
Opius anastrephae Vier	larva	Puerto Rico	native	Anonymous 1938
		Florida	?*	Swanson 1979
Opius bellus Gahan	larva	Florida	Trinidad	Swanson 1979
Opius concolor Szepl.	larva	Florida	France	Swanson 1979
Opius fletcheri Silv.	larva	Puerto Rico	Hawaii	Bartlett 1941
Opius fullawayi Silv.	larva	Puerto Rico	Hawaii	Bartlett 1941
Opius humilis Silv.	larva	Puerto Rico	Hawaii	Bartlett 1941

Table 1--Extended.

Braconidae (cont.)				
Opius perproximus Silv.	larva	Puerto Rico	W. Africa	Bartlett 1941
Opius persulcatus	larva	Florida	Hawaii	Baranowski & Swanson 1971
Parachasma anastrephilum	larva	Florida	native	Marsh 1970
Chalcidae				
Dirhinus giffardi Silv.	pupa	Puerto Rico	Hawaii	Anonymous 1938
		Dominican Republic	Puerto Rico	Anonymous 1939
		Florida	France	Swanson 1979
Cynipidae				
Ganaspis sp.	larva	Puerto Rico	Brazil	Bartlett 1941
Trybliographa daci Weld	larva	Florida	France	Swanson 1979
Diapriidae				
Trichopria sp.	larva	Florida	native	Baranowski & Swanson 1971
Eucoilidae				
Cothonaspis (=Idiomorpha) sp.	larva	Florida	native	Baranowski & Swanson 1971

Table 1--Continued.

Parasitoid	Stage attacked	Location	Source	Reference
Eucoilidae (cont.)				
Eucoila sp.	larva	Puerto Rico	Panama Canal Zone	Bartlett 1941
E. (Pseudeucoila) brasiliensis Ashm.	larva	Puerto Rico	Panama Canal Zone	Bartlett 1941
Eulophidae				
Aceratoneuromyia indicus (Silv.)	larva	Florida	Costa Rica	Swanson 1971
Tetrastrichus giffardianus Silv.	larva	Puerto Rico	Hawaii	Bartlett 1941
Pteromalidae				
Pachycrepoideus dubius Ashm.	larva	Puerto Rico	native	Anonymous 1939
			Brazil, Panama Canal Zone	Bartlett 1941
Pachycrepoideus vindemiae (Rond.)	larva	Florida	native	Baranowski & Swanson 1971
Spalangia cameroni Perk.	larva	Florida	native	Baranowski & Swanson 1971

Table 1--Extended.

Eulophidae (cont.)				
Spalangia endius Walker	larva	Florida	native	Baranowski & Swanson 1971

* Probable natural introduction.

demonstrated and characterized a sex pheromone produced by males to attract the mature females. The sex pheromone blend was isolated and partially chemically identified (Nation 1977). Field bioassay studies were conducted by Perdomo et al. (1975). Both concluded that virgin A. suspensa males attract virgin females through a volatile sex attractant under field conditions. Female A. suspensa resisted mating a second time as one copulation provides sufficient sperm to fertilize her compliment of eggs (Burk 1983). The mating behavior of laboratory-reared and wild flies was compared by Mazomenos et al. (1977). They found the laboratory stock flies matured and mated earlier than wild flies, and multiple mating of females was common in the laboratory strain, but not in the wild strain under the laboratory conditions. Oviposition behavior of laboratoryreared and wild A. suspensa has been studied and chemical stimuli were found to elicite egg deposition (Szentesi et al. 1979). Foraging behavior for food, mate finding, and egg-laying of A. suspensa and other true flies was reviewed by Prokopy and Roitberg (1984).

Biosteres longicaudatus Ashmead

Systematics. B. longicaudatus, a solitary larval-pupal parasitoid, was described by Ashmead in 1905 based upon specimens collected in the Philippine Islands. B. longicaudatua belongs to the family Braconidae, subfamily Opiinae.

Several varieties of B. longicaudatus were described by Fullaway, primarily based upon color differences (Fullaway 1951, 1953). Beardsley (1961) studied these varieties and found that apart from color there were no structural differences to separate them.

Opius longicaudatus (Ashmead) is a synonym of B. longicaudatus (Fullaway 1947).

Distribution. B. longicaudatus has been reported from Malaya, Thailand, the Philippine Islands, Taiwan, New Caledonia, and was successfully introduced into Hawaii, Costa Rica and Mexico (Clausen et al. 1965). B. longicaudatus was successfully introduced into Florida from Hawaii in 1969 (Baranowski 1974), and into Trinidad (Bennett et al. 1977).

Host range. B. longicaudatus attacks several hosts, in the family Tephritidae. They include Ceratitis capitata (Wied.), Dacus ciliatus Loew (?), D. cucurbitae Coq., D. curvipennis (Frogg.), D. dorsalis Hendel, D. frauenfeldi Sch., D. incisus Wlk., D. latifrons (Hendel), D. limbifer, D. nubilus Hendel, D. pedestris (Bez.) D. psidii (Frogg.), D. tryoni (Frogg.), D. zonatus (Saund.), and Procecidochares utilis (Wharton and Marsh 1978).

Mass rearing in Florida under laboratory conditions was developed by Baranowski and Swanson (unpublished) and later Greany et al. (1976) and Ashley et al. (1976) reported upon life history and mass rearing techniques. There are four larval instars, and the immature stage from egg to adult female took 19-23 days and 18-22 days for adult male, respectively (Lawrence 1975). The immature stages are similar to Opius humilis described by Clausen (1940), and to Diachasma tryoni described by Pemberton and Willard (1918).

Host location behavior was mediated by host-associated fungus (Greany et al. 1977b), and/or by host vibration (Lawrence 1981a). The oviposition behavior of B. longicaudatus has been described by Lawrence (1975). Five day-old A. suspensa larvae were the most suitable hosts for

B. longicaudatus development (Lawrence et al. 1976). The effects of the mutual interference of competing B. longicaudatus females on ovipositional success, mortality, and on progeny sex ratio were evaluated by Lawrence (1981b).

Opius concolor Szepligeti

Systematics. Opius concolor, a solitary larval-pupal parasitoid, was described in 1910 based on specimens that emerged from Dacus oleae (Gmel.), pupae collected in Tunisia by Marchal (Marchal 1910). O. concolor belongs to the family Braconidae, subfamily Opiinae. Varieties in O. concolor due to different host species were studied by Fischer (1958). No differences due to the different host flies, D. oleae and C. capitata, were found.

The synonyms of O. concolor are

Opius fuscitarsus Szepligeti, 1913

Opius perproximus Silvestri, 1914

Opius humilis Silvestri, 1914

Opius siculus Monastero, 1931

Distribution. This is a Mediterranean species, originally described from North African-Algeria, and is distributed over Libya, Morocco, Tunisia, Sicily, Tripoli, France, Greece and Italy (Delassus 1924).

Host range. O. concolor attacks D. oleae Gmel., C. capitata Wied, Carpomyia incompleta Becker, and Capparimyia savastini Martelli (Stavraki-Paulopoulou 1967).

Biology. O. concolor mass rearing techniques for laboratory culture in Antibes were developed by Delanoue (1960, 1961). He concluded O. concolor had three larval instars with the immature stage lasting 14 days at 25°C (Delanoue 1960). The third instar larvae of C. capitata were

used as hosts in the laboratory colony in France (Delanoue 1961). Cals-Usciati (1972) later determined after a detailed study of the internal anatomy of the larvae that O. concolor actually had four larval instars. The field biology of O. concolor was studied by Arambourg (1962, 1965). Fernandes (1973) described its immature stages while Cals-Usciati (1966) examined the internal morphology of immature larval stages. The biotic potential, fecundity, and longevity of O. concolor were influenced by temperature, host diet, and mating situations (Stavraki-Paulopoulou 1967). Host preference studies by Biliotti and Dalanoue (1959) indicated O. concolor adult females preferred Dacus to Ceratitis.

Trybliographa daci Weld

Systematics. Trybliographa daci, a solitary larval-pupal parasitoid, was described by Weld in 1951 based on specimens that emerged from Dacus umbrosa F. collected in Malaya. Trybliographa belongs to the family Cynipidae, superfamily Cynipoidea. Cothonaspis Hartig 1841 (Ashmead 1903) is a synonym of the genus Trybliographa Forester 1869.

Distribution. T. daci is distributed over Malaya, northern Queensland, south India, and northern Boreno (Clausen et al. 1965). It was introduced into Hawaii from 1949 to 1951, but the establishment of the species was not successful (Clancy et al. 1952, Weber 1951).

Host range. T. daci has been reared from Dacus umbrosa, D. jarvisi (Tryon), D. tryoni, and D. dorsalis (Weld 1951, Clancy et al. 1952).

Biology. Little has been reported concerning T. daci in the laboratory or in the field. Within the genus Trybliographa, only T. daci and T. rapae (Westwood) have been studied. The complete life cycle of T. daci and its relationship with A. suspensa were studied by Nunez-Bueno

(1982). There are four larval instars, and the duration of development is 26-27 days for males and 28-29 days for females (Nunez-Bueno 1982). The searching behavior of T. daci and the morphology of its eggs and first instar were described by Clausen et al. (1965).

Dirhinus giffardii Silvestri

Systematics. Dirhinus giffardii, a solitary pupal parasitoid in the family Chalcidae, was described by Silvestri in 1914 from specimens that emerged from the Mediterranean fruit fly, Ceratitis capitata, collected in West Africa (Silvestri 1914).

Distribution. D. giffardii has been reported from West Africa, South Africa, Australia, north and south India, Kenya, Nyasaland, and Nigeria (Thompson 1954). It has been introduced into Hawaii and Italy (Thompson 1954). It is one of three fruit fly parasitoids common to both Africa and Indo-Australasia. The other two are Spalangia afra Silv. and Pachycrepoideus vindemmiae (Rond.) (Clausen et al. 1965).

Host range. D. giffardii has been reared from Ceratitis capitata Wied., Ceratitis sp., Dacus cucurbitae, D. oleae, Glossina brevipalpis Newst., G. morsitans Westw., G. palpalis R.-D., and D. dorsalis (Thompson 1954).

Biology. Dresner (1954) briefly described the biology of D. giffardii. He determined that duration of the larval stage is 10-12 days (Dresner 1954). Adults parasitize fruit fly pupae younger than eight days old. According to Silvestri's report, these adults may live for at least five months (Dresner 1954). D. giffardii can act as a hyperparasitoid on Biosteres vandenboschi (Full.) as well as a primary parasitoid on Dacus dorsalis, since D. giffardii is not host-selective (Dresner 1954).

The Interrelationships Between Host and Parasitoid

A parasitoid often emerges in a habitat far from potential hosts, causing the female to seek suitable environment for her progeny (Salt 1935, Doutt et al. 1976). The successful location of hosts by the parasitoid depends on a number factors. With reference to the findings of Salt (1935) and Flanders (1953), Doutt (1964) divided the process necessary for successful parasitism into four steps, including (1) host habitat finding; (2) host finding; (3) host acceptance; and (4) host suitability. Vinson (1975) grouped the first three steps collectively as the host selection process. He also added a fifth step, host regulation (Vinson 1975).

Host Selection Process

The subject of host selection has been reviewed by Doutt (1959) and Vinson (1975, 1976, 1977). A series of cues are involved in the host selection process. These cues may independently follow one another, each individually leading the female parasitoid closer to the host. Conversely, a given cue may elicit the proper response only in the presence of essential preceding cues. Thus, the parasitoid may be led to a host through a hierachy of cues emanating from the host's immediate environment, and different stimuli and different concentrations of a single stimulus may be involved (Vinson 1977). Whether the female parasitoid responds to a series of independent cues or a hierarchy of cues, each succeeding step serves to reduce the distance between it and its host, thereby increasing the potential for encounter.

Habitat finding may be mediated by physical factors such as temperature, humidity, and light intensity (Doutt 1964). The volatile chemical cues important in host habitat location could come from the

host's food (plant, artificial medium), the host itself, stimuli resulting from the host-plant relationship (host-damaged plant), the host-associated organisms, or a combination of these cues (Vinson 1981). All the cues vary with the insect species. For example, Greany et al. (1977b) found that B. longicaudatus is attracted to ethanol and acetaldehyde produced by fungi associated with tephritid fruit fly larvae.

Host locating (i.e., host finding) is defined as a parasitoid's perception of, and orientation toward, a host from a distance through responses to stimuli directly associated with the hosts or host products (Weseloh 1981). Once the female parasitoid has reached a potential host habitat, she must begin a systematic search for the host. To assist it in this search process, the parasitoid relies on short-range chemical or physical cues either emitted directly by the host or associated with its activities (Vinson 1975, 1976; Greany et al. 1977b). Among the chemical cues, kairomones are of primary importance. Weseloh (1981) divided the mechanisms whereby parasitoids use kairomones to find hosts into two categories: long-range and close-range chemoreception. The former is the detection of chemicals in the air by olfaction; the latter is the perception of chemicals by direct physical contact. The physical stimuli involved in host finding are vision, sound, and infrared radiation (Weseloh 1981). Detection of hosts by some parasitoids may be primarily by visualization. Host movement or host sound seems to be the most important stimulus in finding the concealed hosts. B. longicaudatus locates hosts through the detection of host sound/vibration (Lawrence 1981a).

Host detection is typically followed by a decision as to its suitability for oviposition (host acceptance). Weseloh (1974) defined host acceptance as the process whereby hosts are accepted or rejected for oviposition after contact has been made. Host acceptance involves two steps, host selection and host discrimination. Host selection is the choice between hosts of different species or at varying stages of development (Vinson 1976, Arthur 1981). Host discrimination refers to the ability of a parasitoid to distinguish unparasitized from parasitized hosts and thus avoid or choose superparasitism and/or multiparasitism (Salt 1934, van Lenteren 1981). Superparasitism results when parasitoids of one species deposit more eggs in or on the same host than can develop in that host (van Lentern 1981). Multiparasitism is the simultaneous parasitization of a single host by two or more different species of primary parasitoids (Doutt 1964).

Parasitoids are assisted in host discrimination by their ability to detect when a host has been previously attacked. Based on the study of Trichogramma evanescens Westwood, Salt (1937) was the first to report that in the process of depositing eggs in or on the host, the parasitoid left a distinguishable mark. This mark inhibited further attack. Flanders (1951) coined the term "spoor effect" when he suggested that this differentiation may result from an odor left on the host by the parasitoid which previously attacked it. Other inhibitory effects have been termed trail odors (Price 1970), search-deterrent substances (Matthews 1974), deterrent pheromones (Greany and Oatman 1972b) and host-marking pheromones (Vinson 1972, Vinson and Guillot 1972).

The importance of antennae (Spradbery 1970; Greany and Oatman 1972a,b) and the ovipositor (Hays and Vinson 1971, Vinson 1975, van

Lenteren et al. 1976) in host seeking has been reported. A number of parasitoids have chemoreceptors on the ovipositor (Fisher 1971). For example, two types of sensilla on the ovipositor of B. longicaudatus have been identified (Greany et al. 1977a).

Host Suitability

A successful host-parasitoid relationship will not be achieved if the potential host is immune or otherwise unsuitable to the foreign intruder (parasitoid). Therefore, once the parasitoid has located the potential host habitat and selected the host for attack, the development of a new generation depends on the suitability of the host for parasitoid growth (Vinson and Iwantsch 1980a). A suitable host was defined by Salt (1938) as one in which the parasitoid can generally reproduce fertile offspring. Vinson and Iwantsch (1980a) concluded that the successful development of a parasitoid depends on several factors, including (a) evasion of or defense against the host's internal defensive system; (b) competition with other parasitoids; (c) the absence of toxins detrimental to the parasitoid egg or larva; and (d) the host's nutritional adequacy.

The most often described host immune system is encapsulation. This system involves a cellular defensive reaction in which many hemocytes surround and isolate any invading foreign material. The literature concerning insect immunity has been reviewed adequately by Kitano (1969), Nappi (1975), Salt (1968, 1970a,b, 1971), Vinson (1977) and Whitcomb et al. (1974); however, little is known about the mechanisms involved. A parasitoid can avoid encapsulation of its progeny by careful placement of them within certain tissue of the host (Vinson 1977). Eggs deposited by Perilampus hyalinus Say in internal organs such as ganglia of ventral nerve cord, Malphigian tubules, or silk glands of Neodipron

lecontei (Fitch) had a high percentage of survival compared to those eggs located in the hemocoele (Hinks 1971). Additionally, the host's stage of development can affect this immune system. Generally, the effectiveness of the defense mechanism increases with age--the younger host has a relatively weak ability to encapsulate foreign material (Salt 1961; Puttler 1961, 1967; Lynn and Vinson 1967; Lewis and Vinson 1971; Nunez-Bueno 1982). For example, Trybliographa daci was found less encapsulated in younger hosts (Nunez-Bueno 1982). A third way a parasitoid could avoid encapsulation is through its internal defenses. For example, Psuedocoila bochei Weld avoids encapsulation by Drosophila melanogaster Meig. possibly through an inhibitory substance coating its eggs. Some speculate this suppresses the formation of the host's lamellocytes. Alternatively, the inhibitory material might be injected by the female P. bochei during oviposition (Walker 1959, Salt 1968, Streams and Greenberg 1969, Streams 1971).

The inhibition or evasion of the immune response appears related to the constituents of the fluid portion of the calyx region of the reproductive tract (Salt 1955, 1973; Vinson 1972, 1974). Vinson and Scott (1975) concluded that the major portion of the calyx fluid of parasitoid Cardiochiles nigriceps Viereck consisted of small virus-like particles. Edson et al. (1980) found virus particles in the calyx of Campoletis sonorensis (Cameron) which suppressed the encapsulation of the parasitoid's eggs by host Heliothis virescens (F.).

In 1918 Pemberton and Willard reported that larvae of the chalcid Tetrastichus giffardianus Sil. always met a lethal defense reaction in larvae of Dacus cucurbitae Coq. so that they could never develop alone in those hosts. However, whenever a larva was previously parasitized by

Opius fletcheri Sil., an opiine braconid, Tetrastichus was able to develop in it. Pemberton and Willard (1918) assumed that the toxic substance injected into the host larvae by the female O. fletcheri weakened resistance of the Dacus larvae to T. giffardianus. Bess (1939) thought that the resistance of O. fletcheri could be attributed to the toxic substances associated with the parasitoid egg or larva. Salt (1968, 1971) suggested that the resistance was due to the attrition of the host by the opiine larvae and that its teratocytes impeded the defense reaction of the host and allowed the Tetrastichus to escape encapsulation. The mechanism, however, still remains without satisfactory explanation. A similar phenomenon was identified in Pseudeucoila mellipes (Say). When this parasitoid attacked the host Drosophila melanogaster alone, it was encapsulated. However, if P. bochei was parasitized in the same Drosophila host, P. mellipes survived (Walker 1959, Streams and Greenberg 1969, Streams 1971).

Some materials that suppress part of the host defense are very species-specific. P. bochei is not encapsulated in D. melanogaster but is in D. busckii and D. algonquim (Streams 1968). C. nigriceps is not encapsulated in H. virescens but is in the closely related H. zea (Lewis and Vinson 1971). However, the species-specific material does not turn off the complete system, since parasitized H. virescens larvae can still encapsulate certain other foreign objects (Vinson 1972).

Host suitability may also be influenced by the host's age, size, density and nutritional quality; sex ratio; environmental factors; and insect development hormones such as JHA and ecdysones as well as insect growth regulators (Vinson and Iwantsch 1980a).

Host Regulation

The ability of a parasitoid to survive within a host may also depend on its capacity to regulate the host's development for its own needs. Morphological, physiological, or behavioral changes in the host, whether caused by the oviposition females or her progeny, are referred to as host regulation (Vinson and Iwantsch 1980b).

The sources for host regulatory substances are somewhat indistinguishable from those for host suitability. Generally, it is not known which of the changes in the host are a result of "venoms" injected by the ovipositing female or toxins from the egg and developing parasitoid larva. In some parasitoid species, the responsible agent appears to be a symbiotic virus associated with the female parasitoid (Vinson and Scott 1975, Stoltz and Vinson 1979, Vinson et al. 1979).

A successful oviposition is often attained by a parasitoid through reducing the growth of its host. For example, Chelonus insularis Cresson reduces the growth of its hosts H. virescens (F.) and Spodoptera ornithogalli Guenee through the injection of fluids from the parasitoid's calyx and/or poison gland (Ables and Vinson 1981). Microplitis croceipes (Cresson) injects a virus into the host that elevates the trehalose level of the hemolymph and reduces the growth of the host (Dahlman and Vinson 1975). Other examples are provided by Vinson and Iwantsch (1980b).

The Interrelationships Between Parasitoids

Natural communities usually include assemblages of species. Therefore, various interactions between species may occur. When individuals of the same or different solitary parasitic species appear in or on the

same host, competition determines which individual or species will survive.

Competition

The word "competition" is rooted from the Greek, "com," meaning "together" and "petere," meaning "to seek." It indicates a relationship between organisms in which usually only one of the associated parties is benefited. Birch (1957) said, "Competition occurs when a number of animals (of the same or different species) utilize common resources the supply of which is short; if the resources are not in short supply, competition occurs when the animals seeking that nevertheless harm one another in the process." (p. 5) Emlen (1973) modified Birch's definition of competition: "(Interspecific) competition occurs when two or more species experience depressed fitness (r or K) attributable to their mutual presence in the area." (p. 306) By "harm" is meant that the fitness of the population--either its net intrinsic rate of growth (r) or maximum carrying capacity (K)--is lowered from what it would be in the absence of interspecific competition. When competition occurs within the same species, it is called intraspecific competition; when different species are involved, it is called interspecific competition.

Competition is a widespread biological phenomenon which is characterized by two components: exploitation and interference (Park 1962). Exploitation occurs when the organism draws upon a particular resource which is present in limited supply. The more limited the resource and the larger the population draining it the greater is the intensity of competition. Interference occurs when interactions between organisms affect their reproduction or survival. It takes place when the

resource is not in short supply, but when the animals seeking that resource nevertheless harm one another.

Organisms compete for food, shelter, or any other requisite within an ecological niche. Host availability can also be a limited resource and result in competition between parasitoids.

Intraspecific Competition

Nicholson (1954) labelled two forms of intraspecific competition "scramble" and "contest." In both cases there is no competition at low densities--all individuals have as much as they need, and all individuals need and get the same amount. When the population exceeds a threshold density of T individuals, however, the situation changes. In "scramble" competition, all the individuals still get an equal share, but this is less than they need, and as a consequence they all die. In "contest" competition, the individuals fall into two classes when the threshold density (T) is exceeded: T individuals still get an equal and adequate share of the resources, and survive; all other individuals get no resources at all, and therefore die.

"Scramble" and "contest" can be expressed in terms of fecundity. Below T threshold, all individuals produce the maximum number of offspring. Above T threshold, "scramble" leads to the production of no offspring, while "contest" leads to T individuals producing the maximum number of offspring and the rest producing none at all. Intraspecific competition leads to quantitative changes in the numbers surviving in the population and to qualitative changes in those survivors. The quality declines as density increases and competition intensity increases. In nature, the variability of the environment and individuals limits the occurrence of sudden threshold densities.

Intraspecific competition, in the form of superparasitism, occurs when members of the same species are unable to distinguish between healthy and parasitized hosts and thus distribute their progeny at random among the hosts available without reference to previous parasitism (Salt 1934). Failure of oviposition restraint might also cause superparasitism, especially when the supply of hosts is limited (Salt 1934, 1937). Oviposition restraint is the ability of the gravid female parasitoid to refrain from oviposition until it finds an unparasitized host (Salt 1934). The disadvantage is that the life of the parasitoid is limited and restraint from ovipositing in already parasitized host decreases her fitness even more.

The only benefit of superparasitism is a possible reduction in the likelihood of encapsulation by the host (Askew 1971). The disadvantage of superparasitism is the reduction in the reproductive success of the parasitoid. Eggs or hosts are wasted when supernumerary individuals are eliminated or fail to develop normally. Time may be lost while the female oviposits in previously parasitized hosts. Additionally, available hosts may be unutilized (Salt 1934, Askew 1971).

A great deal of evidence indicates that parasitic Hymenoptera belonging to several families tend to avoid superparasitism, but much of the evidence is based upon the non-random distribution of parasitoid eggs in available hosts (Jenni 1951, Force and Messenger 1965, Schroeder 1974, Jorgensen 1975, Rogers 1975).

Observations of superparasitism do not necessarily indicate that a given parasitoid lacks the ability of host discrimination and oviposition restraint (van Lenteren et al. 1978, van Lenteren 1981). Instead, these mechanisms may weaken as the ratio of parasitoids to unparasitized hosts

increases (Salt 1934, Simmonds 1943). Therefore, the observation of superparasitism through behavior is suggested by van Lenteren et al. (1978). Van Lenteren (1981) estimated that 150-200 species of hymenopterous parasitoids have the capacity to discriminate among hosts.

Interspecific Competition

Through interspecific competition one species may cause an increase or a decrease in the fitness of another species, or may have no effect at all. Two contrasting types of interspecific competition were suggested by Park (1954), "interference" (i.e., aggressive) competition and "exploitation" competition. The definitions of these two types of competition were mentioned earlier. Unlike "interference" competition, in "exploitation" competition there is consumption of a limited resource and the reciprocal exclusion of the interacting species may result in the depletion of a resource by one species to a level which makes it essentially valueless to the other species (Begon and Mortimer 1981).

The intensity of interspecific competition is directly related to the degree of ecological similarity (ecological identity) between the species involved. Competitive displacement occurs when different species have identical or very close ecological niches and cannot coexist for long in the same habitat. An example is fruit fly parasitoids in Hawaii. Biosteres longicaudatus Ashm. was first introduced into Hawaii to control Dacus dorsalis Hendel and increased rapidly following its release in 1948. In late 1949, it lost its dominant role to Biosteres vandenboschi. The latter species was replaced by B. oophilus (Full.) during 1950. Each of these replacements was accompanied by a higher total parasitization and a greater reduction in fruit fly infestation. By late 1950 both B. longicaudatus and B. vandenboschi had nearly

disappeared from the field (van den Bosch and Haramoto 1953, Doutt and DeBach 1964).

In some instances, competitive replacement is independent of host density. Instead, it is influenced by the condition of the host species--the host may provide a more suitable environment for one parasitoid than its competitor. The replaced species is therefore intrinsically inferior. In other situations, the replacement of one species by another is affected by host density. Unlike the replaced species, the surviving species is successful at locating a host even when the number of suitable hosts is limited. The replaced species is extrinsically inferior (Flanders 1966). Coexistence occurs only when the interacting species utilize the common resource differently.

Study of interspecific interactions will help in structuring the r-K continuum parasitoid guild which reveals how the interspecific competitive abilities of parasitoid larvae are related, as well as the parasitoid reproductive potential (Price 1973a,b; Force 1974).

K- and r-selection were coined by MacArthur and Wilson (1967). The K, or carrying capacity, refers to the selection for competitive ability in crowded populations. The r, or the maximal intrinsic rate of natural increase, refers to the selection for high population growth in uncrowded populations. Force (1972) suggested that parasitoid complexes are likely to range on a continuum from those species with high reproductive ability (r strategists) in the early stages of succession, to those with high competitive ability (K strategists) as succession proceeds to provide more stable conditions. Certainly, no organism is completely "r-selected" or "K-selected," but all must reach some compromise between the two extremes. Thus, an r-K continuum can be visualized (Pianka 1970, Force

1974). The r-endpoint represents the quantitative extreme: a perfect ecological vacuum, with no density effects and no competition. The K-endpoint represents the qualitative extreme: density effects are maximized and the environment is saturated with organisms. K-selection leads to increasing efficiency of utilization of environmental resources. Even in a perfect ecological vacuum, as soon as the first organism replicates itself, there is the possibility of some competition. Natural selection should therefore favor compromising a little more toward the K-selection. Hence, as an ecological vacuum is filled, selection will shift a population from the r- toward K-selection (MacArthur and Wilson 1967).

In the case of multi-species introduction, an r-K continuum exists among the parasitoids. It would be helpful to know the competitive relationships between the various species so that the most r-selected parasitoids could be imported and colonized first. The more K-selected species could then be colonized at a later date. Hence, pre-introduction studies of natural enemies for assessing competitive interactions among members of a parasitoid guild have been suggested (Watt 1965, Pschorn-Walcher 1977, Ehler 1979).

The r-K continuum provides an index of the potential reproductive capacity and the intrinsic competitive ability of the species involved. The information is expressed in only relative terms, however. When any new species is introduced or any species disappears, the positions of each species shift. Therefore, although the concept of K- and r-selection provides useful insight into evolutionary ecology, its overall utility in biocontrol may be somewhat limited. The relationship between intrinsic competitive ability and relative reproductive potential

is established, but this is not sufficient to predict which particular natural enemy will be dominant (Miller 197").

The concept of r- and K-selection has been responsible for stimulating much of the recent research into life history patterns. However, there are many dimensions to a life history pattern in addition to the r- and K-selection which must be considered before attempting to predict the successful establishment of an imported species (MacArthur 1972, Wilbur et al. 1974, Bierne 1975, Boyce 1979, Whittaker and Goodman 1979). The r-K concept is merely one of many predictive tools.

Mechanisms of Competition

Supernumerary parasitoids may be eliminated in two ways: (1) physical attack, in which a 1st instar parasitoid uses its mandibles to attack a competitor; and (2) physiological suppression caused by a toxin, anoxia, or nutritional deprivation (Salt 1961, Fisher 1971). Selective starvation and accidental injury have also been suggested as means of physiological suppression (Salt 1961, Klomp and Terrink 1978).

A physical attack or cannibalism, using the mandibles, by one parasitoid larva on another is a common phenomenon among solitary endoparasitoids. Many species of parasitic Hymenoptera have sharply pointed or sickle-shaped mandibles in their first instar, and with these they attack other parasitoids present in the same host. Observations of physical attack have been recorded in the major families of parasitic Hymenoptera: Ichneumonidae, Braconidae, Eulophidae, Cynipidae, Chalcidae, Encyrtidae and Scelionidae (recorded by Vinson and Iwantsch 1980a). The newly hatched B. longicaudatus larvae actively move about the host haemocoel attacking other parasitoid larvae they encounter with their mandibles (Lawrence et al. 1976). A similar process was observed in T.

daci in which the victim ceased to feed and was eventually encapsulated by the host's phagocytic blood cells while the victor resumed feeding and growing (Nunez-Bueno 1982).

In many cases of competition between supernumerary parasitoids no evidence of physical attack--such as scars on the victim's cuticle, is observed. It has generally been assumed that the victim's death then is due to some physiological suppression caused by the competing larvae. The physiological suppression may be achieved by conditioning the haemolymph of the host so that it becomes unsuitable for the development of any successor. This may occur during embryonic development, egg hatch, or larval development (Vinson 1972). Alternately, the suppression may be the result of the secretion of toxic substances which kill the opponent (Timberlake 1910, 1912; Pemberton and Willard 1918; Fisher and Ganesaligam 1970; Fisher 1971; Vinson 1975).

Other means of physiological suppression have been identified. Through anoxia, it appears the respiratory requirements of the younger parasitoids are not satisfied in hosts containing older larvae. The young ones therefore die from lack of oxygen (Simmonds 1943, Lewis 1960, Fisher 1963, Edson and Vinson 1976). In some cases the older parasitoid is presumed to survive by eliminating the younger through starvation (Klomp and Terrink 1978). Changes in fecundity, longevity, size and sex ratio may be due to food shortage (Chacko 1964, 1969; Wylie 1965). Finally, the venom or virus-like particles injected by the ovipositing females may result in the change in physiology of the host and cause an unsuitable environment for the younger competing parasitoids (Fisher and Ganesalingam 1970, Guillot and Vinson 1972, Dahlman and Vinson 1975, Sroka and Vinson 1978, Edson et al. 1980).

CHAPTER III
BIOLOGICAL AND REPRODUCTIVE CHARACTERISTICS OF INTERACTING SPECIES

In order to be effective in finding and utilizing their host insects, parasitoids are thought to be dependent upon certain basic biological, morphological, and physiological characteristics. DeBach (1974) suggested criteria for "best" parasitoid; among those suggested the most important ones are (1) searching efficiency--the ability to locate and successfully parasitize the host; (2) reproductive potential--the higher the better; and (3) physiological tolerances similar to those of the host. In addition to these basic attributes, parasitoids often possess other complex and diverse characteristics. Some characteristics of parasitoids may not meet the "best" parasitoid criteria, but may provide unique opportunities for competition, both intraspecifically and interspecifically. These diverse characteristics are considered adaptive strategies (Force 1972; Price 1973a,b, 1975).

In the present chapter, some morphological (length of ovipositor, type of mouth parts), biological (female longevity, duration of immature stages), reproductive (sex ratio, number of ovarioles, number of eggs), physiological (encapsulation by host) and behavioral (preference of oviposition site, superparasitization) characteristics of the parasitoids are discussed.

Material and Methods

All insect colonies were reared and experiments were carried out at 25±2° C, 70±10% RH and photoperiod of 12:12L.D. at University of Florida, Tropical Research and Education Center, Homestead, Florida.

Insects

A. suspensa was reared in a sugarcane bagasse base medium developed by R.M. Baranowski (unpublished) following the rearing procedures outlined by Burditt et al. (1975).

Five to six day old host larvae confined in 13.5 cm diameter "sting units" (Greany et al. 1976) were separately exposed to B. longicaudatus, O. concolor and T. daci in three 38 x 34 x 20 cm cages for 24 hours. Adult parasitoids were supplied honey, water, and sugar cubes. Host larvae were removed from the sting units after the exposure period and put into moist vermiculate to pupate.

Two to three day old host pupae confined in a 8 cm diameter petri dish were exposed to D. giffardii for five-six days in a 38 x 34 x 20 cm cage. Host pupae were removed after exposure and put into moist vermiculate until emergence.

The original laboratory culture of B. longicaudatus (BL) was obtained from the USDA, Fruit Fly laboratory, Honolulu, Hawaii, in 1969. The cultures of O. concolor (DC), T. daci (TD) and D. giffardii (DG) were obtained from Institute de Researches Agronomiques Tropicales et des Culturales Vivrieres (IRAT), Antibes, France, in 1979.

Morphology and Development Studies

Seventy-five, 5-6 day old A. suspensa larvae confined in 9 cm diameter sting units were exposed to 10 pairs of 4-5 day old parasitoids

of each larval species for 2 hours and then removed. One hundred, 2-3 day old pupae were exposed to 20 pairs of D. giffardii for 2 hours. Dissection of exposed larvae or pupae started 24 hours after the exposure period. The duration and morphology of developmental stages were described and recorded. Some parasitized samples were kept until adults emerged. About 50% of the reared sample were kept individually in No. 00 capsules for additional studies.

Reproductive Capacity Study

One female and one male of each parasitoid species were then introduced into an 8 cm diameter petri dish and provided with honey, water and sugar cubes until they mated. The mated females were used for the following studies: Seventy-five, 5-6 day old host larvae confined in a 9 cm diameter sting unit were exposed to a single 4-5 day old mated female of each larval parasitoid species in three 20 x 20 x 20 cm cages for 24 hr. Ten, 2-3 day old host pupae were also exposed to a single female DG in a 4 cm diameter petri dish for 24 hours. Samples of host larvae were dissected 72 hours after the exposure period with use of a 0.8% saline. The number of eggs found in the parasitized hosts, number of parasitized hosts, and number of superparasitized hosts were recorded. There were five replicates for the larval parasitoid species (BL, OC, and TD), and nine for DG.

The number of eggs and ovarioles were recorded from dissections of 4-5 day old mated females that had never been exposed to hosts.

Fifty host pupae parasitized by mature virgin females were held in a 8 cm diameter petri dish until adult emergence in order to determine the sex of the offspring.

Preference of Oviposition Site

Before each dissection, the mark(s) or scar(s) of the oviposition site were recorded on a prepared chart (Fig. 1). The figure was divided into five areas: the cephal end (CE); caudal end (CAU); and central I (CI); central II (CII); and central III (CIII). Chi-square tests were used to analyze whether or not the parasitoids were selective in adopting a particular site for the placement of their eggs.

Results and Discussion

Morphology and Development Study

The comparative morphology and biology of each species during development are given in Fig. 2 and Table 2. All the newly laid eggs were transparent, and generally turned white and enlarged during development of the embryo. The eggs' similarity in shape, size and color suggested that no dissection should be made within 48 hr after exposure in order to avoid errors in counting. DG's eggs were visible through the puparium since they were laid attached to the puparium and outside the true pupa.

Both BL and OC have caudate/mandibulate type first instar larvae, bearing sickle-like mandibles. The heads are large, heavily sclerotolized and brownish in color. The serosal cellular mass still clings to the ventral surface. The head of OC is somewhat squarer than that of BL, with much darker colored mandibles and cephalic edge of the sclerotolized front portion. The integumental folds of the body segments are usually compressed and dark brown in OC. In contrast, the integumental folds in BL are distended and almost transparent or light brown. Hymenopteriform type larvae are common in the second and later

Fig. 1. Oviposition site chart.

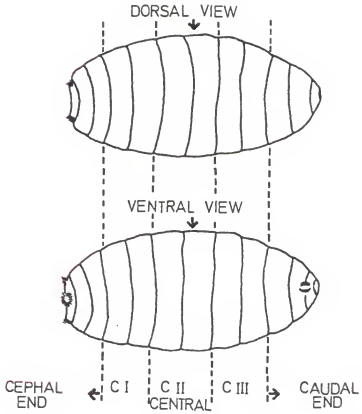

DORSAL VIEW
VENTRAL VIEW
CEPHAL END
C I
C II
CENTRAL
C III
CAUDAL END

Fig. 2. Morphological characteristics of immature stages of BL, OC, TD and DG.

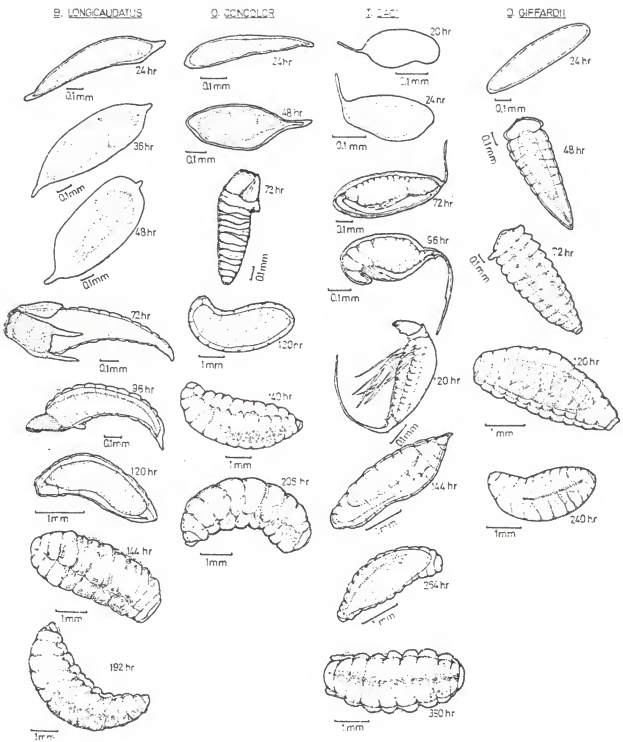

B. LONGICAUDATUS
24 hr
0.1mm
36 hr
0.1mm
48 hr
0.1mm
72 hr
0.1mm
96 hr
0.1mm
120 hr
1mm
144 hr
1mm
192 hr
1mm
Q. SCNCOLOR
24 hr
0.1mm
48 hr
0.1mm
72 hr
0.1mm
120 hr
1mm
140 hr
1mm
205 hr
1mm
I. ZEE
20 hr
0.1mm
24 hr
0.1mm
72 hr
0.1mm
96 hr
0.1mm
120 hr
0.1mm
144 hr
1mm
264 hr
1mm
360 hr
1mm
D. GIFFARDII
24 hr
0.1mm
48 hr
0.1mm
72 hr
0.1mm
120 hr
1mm
240 hr
1mm

Table 2. General morphological and biological characteristics of B. longicaudatus (BL), O. concolor (OC), T. daci (TD), and D. giffardii (DG).

Characteristics	Species			
	BL	OC	TD	DG
Parasitic behavior	larval	larval	larval	pupal
Feeding behavior	internal the pupa	internal the pupa	internal the pupa	external the pupa
Egg	cylindrical with tapering cephalad and caudate	cylindrical with tapering cephalad and caudate	stalked cephalad	ellipsoidal
1st instar	caudate/mandibulate	caudate/mandibulate	eucoiliform	caudate/mandibulate
2nd & up instars	hymenopteriform	hymenopteriform	hymenopteriform	hymenopteriform
Length of ovipositor (cm)	0.55	0.30	0.25	0.25
Female longevity (day)	14-20	10-15	15-18	30-37
Duration of immature (day)	18-22	17-21	27-36	17-20
Duration of egg stage (hr)	36-48	36-48	48-60	36-48

Table 2--Extended.

Duration of 1st instar (hr)	48-72	36-72	48-144	24-48
Superparasitism	yes	yes	yes	rarely
Encapsulation	none	none	yes	none
Other possible lethal factors	--	ring-like structure	--	host-feeding
Sex ratio - ♂:♀	1:2	1:2.4	1:1	1:2.3

instars of these four species; they all are glabrous throughout. The first instar of TD is eucoiliform with three pairs of appendages used in locomotion. The first instar of DG is a caudate type. The larval mandible is a simple, pointed structure lacking subsidiary teeth.

The durations of the first instar and egg stage are important in intraspecific and interspecific competition. The first instar, when the larvae have sharp mouth parts, is the most competitive stage. When parasitoids are present together, the first species hatched has the advantage, and the species having the shorter egg stage is benefited.

The development duration of the immature stages of BL, OC, and DG is more or less synchronized with that of the host (18-24 days) (Lawrence 1975). The duration of development was longer and varied considerably in TD (27-36 days). The possible reason for the variation in the timing of the emergence of TD adults can be assumed to be due to the development of the first instar, which is the stage in which encapsulation is frequently observed, since some encapsulated larvae would escape from further encapsulation after 4-5 days by active movement. Another variation in TD development occurs during the fourth instar which may range from 2 to 15 days (Nunez-Bueno 1982). In the present study the duration of the fourth instar ranged from 2-4 days. However, as a resident of subtropic and tropic areas, A. suspensa has many generations each year and the synchronization of parasitoid and host is not so important as long as the number of available hosts is sufficient.

The longevity of the female is important because the longer the adult life, the greater the number of hosts that can be expected to be encountered. Short-lived species may compensate for the disadvantage

through high reproductive or competitive abilities. Less reproductive species may compensate through an extended life span. In the present study, the longevity of OC was the shortest (10-14 days), and that of BL and TD was similar (14-20 and 15-18 days). DG had the greatest longevity (30-37 days).

Differences in the ages or sizes of hosts concealed in the fruit may be exploited by species with differing ovipositor lengths (Price 1972). Short ovipositors are used in attacking exposed or barely concealed hosts; long ovipositors are needed in attacking a deeply concealed host. Usually A. suspensa larvae feed inside the fruit and approach the skin when they are 5-6 days old and ready to pupate. BL has a longer ovipositor (0.55±0.03 cm) than the other three species. With it, BL can search and out reach the hosts that are barely or deeply concealed. The similarity in the lengths of TD and OC ovipositors--0.25±0.03 cm and 0.30±0.03 cm, respectively--suggested a similarity in host exploitation. If TD and OC searched the same host fruit for A. suspensa larvae, they might have become too closely packed to allow coexistence. The ovipositor length of DG (0.25±0.03 cm) is similar to that of TD and OC, but DG searches for a different niche (pupae) than the larval parasitoids.

Superparasitism was observed in all the studied species. The resultant waste of eggs and reduction in the number of hosts attacked limit the parasitoid's effectiveness as control agents. The impact of superparasitism on the control effect of each species will be discussed further in Chapter IV.

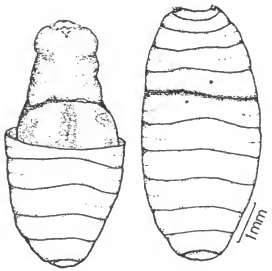
Encapsulation of the first instar of TD was commonly found but not of other species. Fewer capsules were found in superparasitized hosts

and the relationship between encapsulation and superparasitism will be covered in Chapter IV.

Parasitic insects are known to destroy significantly more hosts than they effectively utilize for reproductive purposes through host probing, host feeding and aborted parasitism (DeBach 1943; Flanders 1953, 1973). This may have as great, or greater, impact on the reduction of the host population than parasitization (DeBach 1943; Flanders 1953, 1973; Legner 1979). At low host densities, initial host-destroying activities of the female may so deplete the host population that few individuals remain for later reproduction of the parasitoid. Thus this type of predatory reduction of the host population tends to reduce the controlling capacity of the parasitoid population, because the parasitoid must become more efficient in searching for available hosts. Under conditions of low host numbers the tendency is inimical to survival of the parasitoid, since it increases the number of hosts required to maintain a parasitoid population.

The OC and DG parasitoids provide examples of other behaviors that may be lethal to the host. When the ovipositors of OC females pierced the host without laying eggs, a ring-like structure was formed. A dark brown circle appeared around the puparium, usually between the postcepalic fourth and fifth segments (Fig. 3b). After the puparium was opened, a dark brown line was found on the pupa around the thorax area or the area between the thorax and abdomen (Fig. 3a). The portion above the "ring" would shrink and no fruit fly would emerge from it. This phenomenon may be of selective advantage to the host at very high host densities and at the same time be deleterious to parasitoids because it can suppress the parasitoid population. The quantitative analysis of host-destruction

Fig. 3. Ring-structure damage due to O. concolor.



A. B.

due to ring-structure done by OC will be discussed in Chapter II. Host-feeding behavior was observed occasionally in DG females, usually shortly after the female deposited an egg. The female turned or circled around the oviposition site several times then started feeding from the wound. Feeding lasted no more than 10 seconds. Host-feeding by DG always occurred only after oviposition but was not consistently observed; thus it was difficult to quantitatively measure the host-destruction done by host-feeding.

Parasitoid rearing programs are designed to produce a maximum number of mated females for release; therefore, a population with a female-dominant sex ratio is favored. The ratios of males to females of the adult parasitoids studied were 1:2 (BL), 1:2.4 (OC), 1:1 (TD), and 1:2.3 (DG). BL, OC, and DG had a higher female-dominant sex ratio than that of TD, but the sex ratios might have been altered due to different degrees of intraspecific and/or interspecific competition. This will be discussed in Chapters IV and V.

Reproductive Capacity Study

The reproductive characteristics and the superparasitism of BL, OC, TD, and DG are given in Table 3. Females of all four species continue to produce mature eggs throughout their lives (synovigenisis). A meroistic-polytrophic type of ovariole, in which nutritive cells are located in ovarioles, was found in BL, OC, and DG. In contrast, panoistic ovarioles, those lacking nutritive cells in ovarioles, were noted in TD. This is the case in many Cynipidae (Iwata 1962). With 31-34 ovarioles per ovary, TD has many more ovarioles than the other three species--BL and OC both have two ovarioles per ovary; DG has three. In most chalcid families, ovarioles are rather long and slender and indicate a linear

Table 3. Reproductive characteristics of BL, OC, TD, AND DG.

Characteristics	Species			
	BL	OC	TD	DG
Type of ovarioles	meroistic-polytrophic	meroistic-polytrophic	panoistic	meroistic-polytrophic
No. ovarioles/ovary	2	2	31-34	3
No. mature eggs/ovariole	22-25	12-20	4-5	1-2
No. eggs/ovary $\bar{X} \pm$ S.E.	47.4 ± 2.0 (n=10)	39.8 ± 2.5 (n=11)	146.8 ± 10.4 (n=6)	3.06 ± 0.1 (n=17)
Eggs/ /day $\bar{X} \pm$ S.E.	30.7 ± 5.9 (14-42)	25.7 ± 5.6 (3-37)	55.7 ± 4.7 (50-65)	4.9 ± 0.4 (3-7)
Solitary	yes	yes	yes	yes
Arrhenotoky	yes	yes	yes	yes

series of immature oocytes at their distal portion (Iwata 1962). The three pairs of ovarioles found in DG females each produce one mature egg--and on rare occasions, two eggs--a day. Similar findings were observed in the chalcid pupal parasitoid, Brachymeria intermedia (Nees), of the gypsy moth by Barbosa and Frongillo (1979). A maximum number of six parasitoid progeny were produced by B. intermedia females in a 24-hour period.

In a comparison of ovariole numbers among parasitoid families, Price (1975) found that families (e.g., Ichneumonidae and Tachinidae) that attacked the host in its later stages had fewer ovarioles per ovary. Since the mortality of the parasitoids declined with increased host age, the later the stage attacked the less the need for high fecundity (Price 1975). Those species with high fecundity that attack early host stages may be regarded as r strategists, and those with relatively low fecundity that attack later stages may be considered K strategists (Price 1973a,b 1975; Askew 1975; Force 1975). In the present study, DG had the lowest fecundity compared to the other larval parasitoids. This disadvantage, however, was compensated for by DG's greater longevity. Thus, DG is more K-selection oriented in relation to the three larval parasitic species in terms of host age at times of attack, longevity, and reproductive capacity.

Two pairs of ovarioles are found in both BL and OC. Each ovary contains about 47 eggs in BL and 40 eggs in OC (Table 3). The morphology of ovary and ovogenesis of OC was studied by Stavraki-Paulopoulou (1967). The highest biotic potential as indicated by the number of ovarioles and number of oocytes was noted in TD (Table 3), but this was not necessarily correlated with a high frequency of successful attacks on the hosts.

Instead, heavy encapsulation and a high percentage of superparasitism caused TD's actual success to fall short of its potential capacity. Superparasitism was also observed in the other three species in different degrees.

All four species were found to be absolutely solitary and arrhenotokous, since no more than one parasitoid emerged from any singly isolated pupa, and only males emerged from virgin female parasitized hosts. These results differ from Dresner's (1954) findings on DG. He suggested a somewhat gregarious habit of DG in which more than one parasitoid emerged from a single host puparium.

Preference of Oviposition Site

Although the pupal chart (Fig. 1) shows both dorsal and ventral sides, the statistical analysis used pooled these data as one. The preference results are given in Table 4. Based upon Chi square tests, significant differences in deposition areas were shown in TD (X^2=14.40) and DG (X^2=51.35), but not in BL (X^2=4.79) or OC (X^2=9.17). This indicates that TD and DG are very selective in their oviposition sites.

Insects are very selective when choosing breeding habitats and oviposition sites within these habitats (Hinton 1981). Their selection involves the assessment of a large number of physiological, chemical, and biological factors (Gerber and Sabourin 1984). Some parasitoids may even be very particular in choosing the oviposition site on the host body (Carton 1973). For example, ichneumonid Pimpla instigator F., a parasitoid of Pieris brassicae L. pupae (chrysalids), lays eggs in a selective manner in the central region of the host (second and third abdominal segments) (Carton 1973, 1974, 1978). In this central region

Table 4. Oviposition site preference of different species.

Area	No. of oviposition marks by			
	BL	OC	TD	DG
Cephalic end (CE)	30 (26.85)*	27 (22.40)	20 (25.84)	10 (11.92)
Central I (CI)	38 (41.97)	24 (35.01)	59 (40.40)**	10 (18.63)**
Central II (CII)	45 (40.42)	33 (33.72)	42 (38.90)	8 (17.94)**
Central III (CIII)	43 (36.72)	42 (30.63)**	32 (35.35)	10 (16.30)
Caudal end (CAU)	31 (41.04)	30 (34.24)	27 (39.50)**	45 (18.22)**
Total	187 (187.0)	156 (156.0)	180 (179.99)	83 (83.0)
X^2 (df=4)	4.79	9.17	14.40**	51.35**

* Numbers in parenthesis are the expected frequency.
** Significant difference at 0.05 level by X^2 - test.

the hemocytic reaction is the weakest and thus parasitoid development is most favored (Carton 1973, 1978).

The particularities of diverse egg deposition sites have been assumed to be correlated with the morphology and physiology of the host insects (Flanders 1973). Among three larval parasitoids studied, TD was the only one usually found heavily encapsulated by A. suspensa. It also was the only species selectively depositing eggs in the CI area which is the third and fourth postcephalic segments. Therefore, TD's tendency to select particular oviposition areas could be suspected to be correlated with antihost defense mechanisms.

During adult host emergence, the thorax of the enclosing cuticle split along a line of weakness which in the pupa was T-shaped (Chapman 1971). The line was usually located around the postcephalic third or fourth segments of the puparium. This area probably corresponds to the weakest zone in the larvae. Therefore, it could be preferred by TD for oviposition. Additionally, OC may choose it as the weakest spot on the host for ring-structure damage. The success of TD's preference for depositing eggs in the CI as an anti-host mechanism may be mitigated, however, by the dispersal behavior of its larvae. Hatched TD larvae (as well as those of the other two larval species) usually dispersed within the hemocole and concentrated in the host's abdominal area. Encapsulated TD larvae were frequently found in this area.

Host vibration might also be involved. The head and caudal ends would produce most vibration, and postcephalic may be "safer." Therefore, TD significantly rejected ($X^2=3.96$) caudal area, and the number of oviposition punctures in the cephalic end was less than expected (20 vs. expected 25.84) (Table 4).

The largest difference in oviposition site preference was found in DG, which had a tendency to lay eggs in the caudal area (CAU). DG was the only external feeding species of those studied. Since the larvae developed outside the true pupa, encapsulation was never evident. Thus because of the selective phenomenon, it is logical to conclude that the choice of oviposition site is not due to a physiological association with the host. Instead, a morphological correlation is assumed. The cephal and caudal ends have the shortest distances between puparium and true pupa. DG probably chooses the caudal end instead of the cephalic end because the former is closer to the hemocole. OC had a tendency to lay eggs in the CIII area ($X^2=4.22$), but overall the distribution of oviposition sites was random ($X^2=9.17$). BL showed no preference in oviposition site selection ($X^2=4.79$).

The number of marks on the pupa does not necessarily mean the same number of eggs was deposited. Table 5 shows that the total number of observed scars exceeded the number of dissected pupae and resulted in more than one scar per pupa. This means that the parasitoid had been using her ovipositor in an attempt to discriminate hosts. The host discrimination resulted in an average of one progeny per BL or OC or DG parasitized host. In contrast, significantly more than one egg was found per TD parasitized host ($t=5.40$, $df=31$). It suggested that TD had a tendency to superparasitize hosts while the other species favored healthy hosts.

The location of larvae found inside the hosts was not always associated with the oviposition site. The first instar of DG usually moved to the central portion of the ventral junction of the thorax and abdomen before the first molt. The first instar of the other three

Table 5. The correlation between number of oviposition scars, number of pupae, and number of eggs actually found.

Species	Total no. scars I	Total no. pupae II	Total no. eggs III	No. scars/ pupa I/II	No. eggs/ parasitized host
BL	187	76	67	2.46±2.68* (1-6)	1.10±0.57 (1-5) (n=61)
OC	156	85	55	1.95±2.32 (1-6)	1.12±0.53 (1-4) (n=49)
TD	180	70	66	2.28±2.83 (1-8)	2.06±1.11** (1-6) (n=32)
DG	83	54	39	1.54±1.86 (1-6)	1.08±0.28 (1-2) (n=36)

* $\bar{X}$±S.D.

** Significant difference at p=0.05 by t-test.

species studied usually floated in the hemocoel in the abdominal area. However, in hosts superparasitized by BL, the larvae tended to distribute themselves toward the opposite ends of the host.

CHAPTER IV
OLFACTORY HOST-FINDING STIMULI, HOST DISCRIMINATION, OVIPOSITION RESTRAINT, THE CONTROL EFFECT OF EACH SPECIES, AND THEIR MUTUAL INTERFERENCE

The olfactory stimuli which are associated with the host itself or its host plant play an important role in some parasitoid's host-selection processes (Vinson 1976). In the present study the significance of various host-associated olfactory stimuli was investigated.

Host discrimination is commonly referred to as the ability of a parasitoid species to distinguish between parasitized and non-parasitized hosts and to avoid superparasitism. Statistical analyses have been frequently used to test whether the female parasitoid distributes her progeny randomly among hosts. When the female lays her eggs randomly in the host larvae, the distribution of eggs conforms to a Poisson distribution. A capacity to discriminate among possible hosts is indicated when there is a significant difference between observed parasitoid's eggs and expected random egg distribution. Conversely, superparasitism is considered as failure of the host discriminating ability. Studies by Salt (1934) and Wylie (1965, 1970, 1971a,b, 1972a,b) have shown that superparasitism or multiparasitism is also caused by the failure of oviposition restraint. This occurs when the female has a tendency to oviposit when she encounters only parasitized hosts. In response, she will oviposit in these parasitized hosts. Other possible causes of superparasitism have been summarized by van Lenteren and Bakker

(1975). Van Lenteren et al. (1978) completed detailed observations on other parasitoids' ability to discriminate. This information provided insight into the conditions under which superparasitism occurs. In the present study, the behavioral and statistical aspects of host discrimination were evaluated. An attempt was also made to analyze oviposition restraint and its interrelationship with superparasitism.

Intraspecific competition is a consequence of superparasitism. This results in the elimination of supernumerary parasitoid larvae through combat between larvae or by physiological suppression. Mutual interference between adult parasitoids also affects their reproductive capacity and searching efficiency. Efficiency of a parasitoid can be in the form of avoiding wastage of eggs by discriminating against a host already attacked by a parasitoid. This has been demonstrated by many parasitoids (Doutt 1959, 1964; Salt 1961; Vinson 1976). The present study examined changes in the efficiency of parasitoids when host and parasitoid densities were altered.

Materials and Methods

Egg Distribution Analysis

A. suspensa larvae were presented to the larval parasitoids in 9 cm diameter sting units (Greany et al. 1976). Each unit contained 150±25 host larvae. One hundred, two day old A. suspense pupae were presented to DG in 9 cm diameter petri dishes. Parasitoids and sting units/petri dishes were placed in 38 x 34 x 20 cm cages. Four cages, each with 10 males and 10 females of one of the four parasitoid species, were used for the experiment. Honey, water, and sugar were provided. The host larvae were exposed to each larval parasitoid species (BL, OC, TD) for two

hours. The A. suspensa pupae were exposed to DG for 24 hours. As a controlled observation of A. suspensa's natural mortality under the experimental conditions, one sting unit with host larvae and one petri dish with pupae were set up as described above but were not exposed to parasitiods.

Three to four sting units/petri dishes were present simultaneously in each parasitoid cage. One of the sting units or petri dishes from each cage was used for superparasitism studies and as a control for multiparasitism studies. The remaining units were utilized for the multiparasitism studies described in Chapter V.

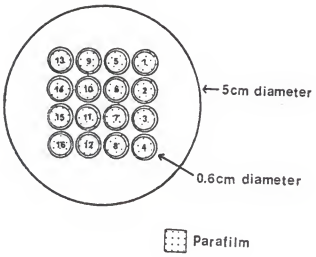
Samples for dissection were taken at intervals of 72-144 hours after exposure, and the remaining samples were reared to adult emergence.

Comparisons of Olfactory Stimuli

If the routine mass rearing procedure had been used, the larvae would have been concealed under a piece of cloth. The cloth, however, would have made the behavioral study of host discrimination more difficult. Parafilm was used instead because of its transparancy and tensibility which can imitate the fruit skin or the cloth. Behavioral observations involving a relatively small number of hosts (16) require stimuli that are sufficiently strong to elicit parasitoid behavioral responses that are strong enough to facilitate the study. Four different possible olfactory attractions were compared.

Sixteen, 5-6 day old host larvae were kept individually in 0.3 cm^2 containers and each was covered with a piece of parafilm. These containers were arranged as shown in Fig. 4 in a 5 cm diameter petri dish. One parasitoid was introduced at a time. Five females were used for each of the four categories compared. The categories included

Fig. 4. Set-up for behavioral study.


13
9
5
1
14
10
6
2
15
11
7
3
16
12
8
4
5cm diameter
0.6cm diameter
Parafilm

larva only; larva plus smashed guava; larva plus artificial larval diet; and larva plus "treated" parafilm. The parafilm in the last category was treated by exposing it in the adult fly colony cage before the experiment. Three subgroups under the larva plus "treated" parafilm category were also compared, based upon 1 hour, 2 hour, and 3 hour exposure periods. The observation period was 90 minutes for each female parasitoid.

The time needed for each parasitoid to initiate searching behavior was recorded. The searching behavior of the female comprises two major behavioral components. First, the female "surveys" the area--the parasitoid walks over the surface of the container with the tips of the antennae tapping. The female then draws up or extends her ovipositor and inserts it into the larva. This is referred to as "probing" behavior. The number of containers surveyed by each parasitoid was recorded as well as the number of containers probed. The repetition of either behavior in the same container was counted only once.

Determination of "Accepted" Attack

Sixteen, 5-6 day old larvae, or 2 day old pupae, were arranged as in the preceding experiment. A female parasitoid of each species was introduced and the duration of each "probing" behavior was recorded. The attacked larva/pupa was removed and immediately replaced by another healthy larva/pupa. The removed samples were dissected after 72 hours. The observation period was 60 minutes, and four replications were done for each species.

Behavioral Observations of Host Discrimination

Sixteen, 5-6 day old larvae, or 2 day old pupae, were arranged similarly to those used in the olfactory experiment. The first female

(A) was introduced and presented to the hosts for 1 hour or until half of the hosts were attacked, then removed. After the female A was removed, either the second female (B) of the same species was introduced, or the female A was re-introduced (rA) after a 2 hour interval. Four replications were completed for each combination.

The number and duration of each "probe" was recorded, and a "threshold" time for egg laying was determined. The two criteria used to establish the threshold time were: (1) the majority of egg laying activity occurred after the threshold time; and (2) in a given number of seconds the female spent probing, the proportion of egg laying probes was greater than those of non-egg laying probes. The "probes" were classified into two categories, the accepted attack and the rejected attack. In the former, the duration of the probe was longer than the threshold time for successful oviposition. In the latter, the duration of the probe was shorter than the threshold time. The conditionsof the hosts when the probe occurred were divided into categories. The first included healthy hosts which had never been attacked by any parasitoid, or which had been "rejected" for attack. The rest of the hosts were assumed "parasitized"--they had been "accepted" for attack by the parasitoid.

Oviposition Restraint Study

A series of low parasitoid to host ratios were provided: 1:5, 1:15, 5:5, and 5:15 for larval parasitoid; and 1:2, 1:4, 5:2, and 5:4 for DG. A control group with a 1:75 ratio for the larval, and a 1:10 for the pupal group was prepared to estimate the maximum eggs each female parasitoid would produce during the study period.

Host larvae were confined in a 3 cm diameter sting unit and exposed to parasitoids in a 9 cm diameter petri dish. Host pupae were presented to DG in a 3 cm diameter petri dish. The exposure period was 24 hours. Each series was replicated six times. Beginning 72 hours after exposure, all the removed samples were dissected.

Mutual Interference Between Searching Parasitoids

Two methods were used to investigate how a parasitoid responds to different host densities. First, one or more parasitoids were exposed to each different host density for the same period of time. Second, one or more parasitoids were presented with an open choice of host densities at the same time. The former method provided information about how the parasitoids allocated time and energy at different parasitoid-host densities. The latter method would seem to mimic conditions in the field, where most parasitoids would probably respond to concentrations of hosts by spending more time searching in highly populated areas than in areas of low host density.

Experiment I. In this experiment, 1, 2, and 4 parasitoids of each species were exposed to different host densities (3, 6, 12, 24, 48) for the same period of time. Host larvae were confined in a 3 cm diameter sting unit and presented to the parasitoid in a 9 cm diameter petri dish for 24 hours.

Experiment II. In this experiment, 1, 4, and 16 parasitoids of each species were provided a choice of different host densities at the same time. Nine centimeter diameter sting units/petri dishes including 2 units of 12, 24, and 48 larvae/pupae, 1 or 2 units each of 3 and 6 larvae/pupae, were placed randomly in a 38 x 34 x 20 cm cage, and exposed to parasitoids for 24 hours.

The parasitoid's behavior consisted mainly of walking, probing, and resting. Walking and any periods of flight were included in the walking classification. Probing was the insertion of the ovipositor which may or may not have led to egg laying. Resting was the time when the insect was stationary, including periods of grooming or cleaning. In addition to those behaviors, circling around and host-feeding were observed in DG. Host-feeding was the period when the parasitoid was feeding on the wound made by probing. Circling around occurred when the parasitoid continuously made 360° turning movements around the pupa. This movement is often observed before and after probing, and this behavior was recorded as separate from the walking behavior in DG. Mutual interference was the behavioral consequence of encounters among parasitoid adults. Parasitoids exhibit three types of behavior following a "contact" with another parasitoid: the parasitoid may show no change in behavior; one or both may fly away or walk off the search area; or both may remain but change their activity patterns. Therefore, the "contact" would alter the frequency with which the insects change their behavior, and disrupt their host selection behavior patterns and, thus, affect the extent to which they oviposit.

Behavioral observations were made from six 15 minute observations within the first 4 hours. At the start of each observation period, a parasitoid in the petri dish or cage was selected at random and observed continuously for 7½ minutes. At the end of this time a second parasitoid was similarly selected and observed for a further 7½ minutes. Where only one parasitoid was present it was observed for the full 15 minutes.

Results and Discussion

Egg Distribution Analysis

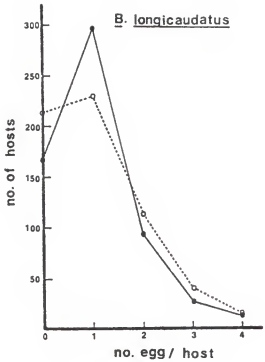
The results of the egg distribution study are given in Table 6 and Fig. 5. The egg distribution of BL, TD, and DG are statistically different from a random distribution. In BL and DG, fewer than expected deposited zero eggs, and more than expected deposited one egg. This information indicates that both species exercise host discrimination. In TD, the significant difference between the expected random frequency and the '0' group was significantly higher than expected. These data, therefore, suggest that TD's host discrimination ability was the reverse of the discrimination displayed by the other three species. Salt (1934) pointed out that any deviation from a random distribution of the progeny would indicate some kind of discrimination. Even if it could be demonstrated that the eggs of the parasitoid were really distributed at random, such a frequency distribution could be due to something other than a random searching behavior. The non-random, aggregated distribution of TD eggs indicates a strong tendency by the parasitoid to lay more than one egg per host (superparasitism). In other words, they discriminated in favor of the parasitized hosts. In fact about 52% of the hosts were superparasitized, with an average 2.43 eggs per host and an average of 3.27 eggs per parasitized host. Superparasitization generally is detrimental to a solitary parasitoid in terms of the wastage of eggs, time, and energy by laying extra eggs in a host. The only advantage of superparasitization could be the avoidance of encapsulation by the host which has a limited supply of hemocytes for encapsulation (Puttler 1967, Salt 1934, Streams 1971). The relationship between TD superparasitization and encapsulation will be discussed in a separate section.

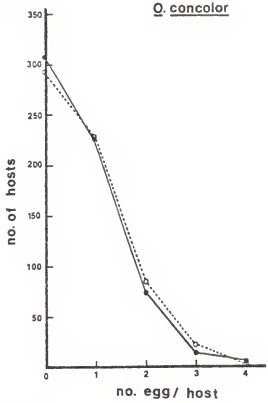
Table 6. The egg distribution of BL, OC, TD, and DG in A. suspensa.

Species		No. host recovered with n parasitoid progeny								Σ	χ^2	% Parasitism (n)	% Superpara-sitism (n)	Parasitoid eggs		
		0	1	2	3	4	5	6	≥7					Total	$\bar{X}$ eggs/ host	$\bar{X}$/parasitized host
BL	obs.	168	298	91	28		13			598	45.00*	71.95±5.52	22.07b**	623	1.04c	2.46b
	exp.	211.0	219.4	114.1	39.6		13.9			598.0		(430)	(132)			
OC	obs.	309	228	73	16		7			633	5.86	51.12±8.92	15.17b	489	0.77b	2.72b
	exp.	292.4	228.9	87.2	22.5		5.1			633.1		(324)	(96)			
TD	obs.	150	127	91	65	43	40	22	45	583	455.66*	73.86±5.72	52.49a	1415	2.43d	3.27c
	exp.	51.5	124.9	151.6	122.7	74.4	36.1	14.6	7.1	582.9		(433)	(306)			
DG	obs.	246	121	12						379	9.45*	33.12±4.59	3.17c	147	0.39a	2.17a
	exp.	257.2	99.8	21.9						378.9		(133)	(12)			

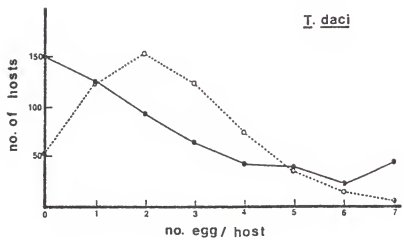
* Indicates the significant difference from Poisson distribution at p=0.05.
** Values followed by the same letter in the same column mean no significant difference by t-test at p=0.05.

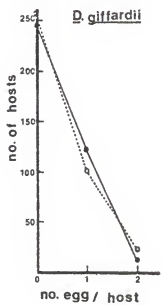
Fig. 5. Frequency distribution of eggs laid by BL, OC, TD and DG.





observed
expected





Varley's (1941) study of five hymenopterous parasitoids of knapweed gallfly, Urophora jaceana Hering, revealed that only Eurytoma tibalis Bugbee exercises host discrimination against superparasitism, while the four other species either distributed their eggs randomly or in an aggregated manner. Varley pointed out that superparasitism is detrimental only if the eggs so wasted might have been laid on unparasitized hosts, and it is really the ability to find hosts, rather than egg supply, which limits the increase in numbers of a parasitoid.

Among the four species examined in this study, DG demonstrated the smallest percentage of superparasitism (3.17%) with an average of 0.39 eggs per dissected host and 2.17 eggs per parasitized host. These figures are significantly smaller than those of other species. BL and OC demonstrated comparable degrees of superparasitism (22.07% and 15.17%, respectively) and a similar number of eggs per parasitized host (2.46 eggs and 2.72 eggs, respectively). However, OC deposited a smaller number of eggs per host (0.77) than BL (1.04). TD exhibited the highest degree of superparasitism (52.49%) among the four species with an average 2.43 eggs per host and 3.27 eggs per parasitized host. Those figures are significantly larger than those of other species (Table 6).

From the examination of the supernumerary individuals of each species after dissection of samples, it was observed that the supernumerary individuals were eliminated by cannibalism or, very occasionally, by physiological suppression, depending on the time interval between the several attacks on the host. Evidence of a physical attack was provided by a melanised scar on the dead larva or egg. When dead individuals without attack scars were found, it was assumed that some physiological suppression was the cause of death. If the

ovipositions were simultaneous, or nearly so, which was the case in this study (2 hour exposure), the larva that hatched first usually attacked and killed most or all of the eggs. It also attacked other newly hatched larva that it encountered and either destroyed them or was itself killed. Rather frequently a parasitoid larva was found with its mouthparts attached to another larva. In only one out of 132 BL superparasitized dissected samples, two BL first instar larvae were dead with scars on their bodies. In one host, heavily superparasitized by OC, all of the 27 larvae died soon after they hatched. This early mortality probably resulted from host unsuitability associated with repeated piercing by the female parasitoids during oviposition and/or from feeding by a large number of parasitoid larvae. In hosts superparasitized by TD, encapsulation was the major means of eliminating supernumeraries. Cannibalism occurred when more than one larvae survived encapsulation.

Multiple attacks by the same or different individuals would destroy the host and consequently many progeny would also die. In a few cases, two BL progeny, two or three OC or TD progeny, all in later instars or the prepupal stages, would survive in a single host. Eventually, however, only one parasitoid adult emerged.

Encapsulation and Superparasitism of T. daci

The distribution of TD progeny and percent of encapsulation (E%) in singly and superparasitized hosts are given in Tables 7 and 8. There was no significant difference in E%, the number of encapsulated TD progeny/ total number of TD progeny x 100, between singly and superparasitized hosts ($t=1.01$, $df=1414$, $p=0.05$). There was a significant difference in the percent of hosts in which all the TD progeny were completely surrounded by hemocytes (HCE%). The HCE% represents the number of hosts

Table 7. Distribution of encapsulation in hosts singly and superparasitized by T. daci.

No. TD per host	No. hosts with n encapsulated progeny														Total host	Total TD	E%*,**	HCE%***
	0	1	2	3	4	5	6	7	8	9	10	12	13	18				
1	11	116													127	127	91.34a	91.34a
2	3	7	81												91	182	92.86a	89.01a
3	1	1	6	57											65	195	94.36a	87.69a
4				6	37										43	172	96.51a	86.05a
5				1	4	35									40	200	97.00a	87.50a
6				1	1	4	16								22	132	93.18a	72.73b
7					1	2	2	12							17	119	92.44a	70.59b
8			1					2	6						9	72		
9									2	4					6	54		
10											5				5	28 50 288	91.32a	71.34b
11									1						1	11		
12									1			2			3	36		
13													3		3	39		
26														1	1	26		

Table 7--Extended.

N			433	1415
Mean±S.D.			93.62±2.17	82.04±8.81

*E%: Percentage of encapsulation = (No. encapsulated TD/Total TD) x 100%.
**Values followed by the same letter indicate there is no significant difference at p=0.05.
***HCE%: Percentage of hosts with TD completely encapsulated = (No. hosts with all TD progeny completely encapsulated/Total TD parasitized hosts) x 100%.

Table 8. Comparisons of E% and HCE% between A. suspensa singly and superparasitized by T. daci.

No. TD/host	Total hosts	Total TD	E%*	HCE%
1	127	127	91.34±28.24 a	91.34±28.24 a
⩾2	306	1288	93.87±24.00 a	80.71± 8.61 b
N	433	1415	t = 1.01	t = 2.59

* Values followed by the same letter in the same column indicate there is no significant difference by Student's t-test at p=0.05.

Table 9. Number of parasitoids emerged from reared samples and the progeny sex ratio.

Species	Total no. of sample I	No. parasitoid emerged II	% parasitoid emergence II/I ($\bar{X}$±S.D.)	Sex ratio ♂:♀
BL (n=38)	4717	1871	39.5±4.5	1:1.9
OC (n=38)	4951	322	6.5±2.1	1:2.4
TD (n=38)	5142	851	16.5±6.5	1:1.0
DG (n=28)	4201	838	19.9±3.7	1:2.3

with all the TD progeny surrounded by hemocytes/total number of TD parasitized hosts x 100% (Table 8). None of these TD had a chance to survive. Therefore (100-HCE) x 100% represents the percent of hosts attacked by TD from which adult TD are expected to emerge. Being a solitary parasitoid, only one TD can complete development in superparasitized hosts no matter how many healthy TD initially existed in the same host. There were no significant differences in E% between the host groups with one TD to eight or more TD parasitoids (Table 7). This indicates that there was no reduction in the degree of encapsulation as the number of TD per host increased. One possible explanation is that the hemocytes of host larvae are sufficient to encapsulate at least as many as 18 TD progeny (Table 7). The superparasitism studies showed that a greater percent of parasitoids emerged from superparasitized hosts than from singly parasitized hosts. These results agree with the finding of Streams (1971) on Pseudeucoila bochei parasitizing Drosophila melanogaster and Puttler (1967) on Bathyplectes curculionis (Thomson) parasitizing Hypera postica (Gyllenhal). Therefore, although superparatism may assist the host in some instances, it also may be used as a defense mechanism by the parasitoids. Antihost immunity substances such as the viroid particles in the calyx of several parasitoids (Stoltz and Vinson 1976, Stoltz et al. 1976) or egg coating material or "venoms" produced by females (findings reviewed by Salt 1968, 1971) have been identified. It could be that TD does not have such antihost immunity substances and must therefore use superparasitism as a mechanism of defense.

Control Effect of Each Species

Results of the experiments on the reared samples of the egg distribution study are given in Table 9. The analysis of mortality factors contributed by each species upon dissection and comparisons with reared samples are given in Tables 10-13. The assumed natural mortality of A. suspensa under experimental conditions was 21.45±6.50% (X±S.D.).

There is a considerable difference in the percentage of parasitism from the dissected samples (DS) and the percentage of F_1 parasitoid emergence from the reared samples (RS) of the four species (Tables 10-13). In the TD group (Table 10), the difference (RS-DS) was about 57% which coincided with the encapsulation percentage from information obtained through dissection (56.47%). Also, the mortality due to the parastitoid estimated through dissection (17.39%) coincided well with the percent parasitoid emergence (16.53%). Those findings indicated that encapsulation can be assumed to be the major cause of the failure of TD progeny to successfully emerge, and parasitism was the main cause of host mortality contributed by TD.

In the other three species no significant evidence of parasitoid mortality factors was found in dissected samples. Only 3.1% of the dead OC progeny showed multiple piercing scars (Table 11). In BL (Table 12) 0.2% of the parasitoid mortality was due to cannibalism, since all the competing dead larvae had scars on their bodies. No parasitoid mortality factor was found in the DG group (Table 13). Therefore, the DS and RS differences are due to unknown factor(s). Some pathogenic factor which might have been introduced during female oviposition, or through the wounds due to probing could be suspected. The fatal effect of this pathogen on the progeny could not have been detected during the

Table 10. Analysis of mortality factors of A. suspensa after exposure to T. daci.

	Mortality category	Mortality factors	$\bar{X}$% ± S.D.
Dissected Samples (DS) n=583	Mortality of host due to parasitoid	Parasitism (I)	73.86±5.72
		Total	73.86±5.72
	Mortality of parasitoid progeny	Encapsulation by host	56.47±8.44*
	Estimated total mortality due to TD		17.39±5.98**
			$\bar{X}$% ± S.D.
Reared Smaples (RS) n=5142	Total mortality (TM)		42.16±3.91
	Natural mortality		21.45±6.50
	Mortality due to parasitoid (TM-21.45) (II)		20.71±4.14**
	% Parasitoid emergence (no. emerged parasitoid/RS) (III)		16.53±2.27**
	Mortality due to parasitoid besides parasitism (II-III)		4.18±4.15
	Difference of parasitism between DS and RS (I-III)		57.33±6.05*

* No significant difference between values with the same marks by t-test p=0.05.

** No significant difference among values with the same marks by t-test p=0.05.

Table 11. Analysis of mortality factors of A. suspensa after exposure to O. concolor.

	Mortality category	Mortality factors	$\bar{X}$% ± S.D.
Dissected Samples (DS) n=633	Mortality of host due to parasitoid	Parasitism (I)	51.12±8.92
		Multi-probing scars, no progeny, host content rotten	5.75±1.65
		Ring-structure	20.86±4.56
		Total	77.73±10.12
	Mortality of parasitoid progeny	With probing scars, progeny found	3.10±0.52
	Estimated total mortality due to OC		74.73±11.18
Reared Samples (RS) n=4951			$\bar{X}$% ± S.D.
	Total mortality (TM)		65.43±7.61
	Natural mortality		21.45±6.50
	Mortality due to parasitoid (TM-21.45) (II)		43.98±8.07
	% Parasitoid emergence (no. emerged parasitoid/RS) (III)		6.47±2.05
	Mortality due to parasitoid besides parasitism (II-III)		37.51±8.47
	Difference of parasitism between DS and RS (I-III)		44.65±9.01

Table 12. Analysis of mortality factors of A. suspensa after exposure to B. longicaudatus.

	Mortality category	Mortality factors	$\bar{X}$% ± S.D.
Dissected Samples (DS) n=598	Mortality of host due to parasitoid	Parasitism (I)	71.95±5.52
		Multi-probing scars, no progeny, host content rotten	8.38±1.85
	Mortality of parasitoid progeny	Ring-structure Cannibalism	1.03±0.04 0.2
		Total	81.04±9.17
	Estimated total mortality due to BL		81.04±9.17
			$\bar{X}$% ± S.D.
Reared Samples (RS) n=4717	Total mortality (TM)		74.45±8.28
	Natural mortality		21.45±6.50
	Mortality due to parasitoid (TM-21.45) (II)		53.00±8.92
	% Parasitoid emergence (no. emerged parasitoid/RS) (III)		39.47±4.48
	Mortality due to parasitoid besides parasitism (II-III)		13.51±9.12
	Difference of parasitism between DS and RS (I-III)		32.46±6.71

Table 13. Analysis of mortality factors of A. suspensa after exposure to D. giffardii.

	Mortality category	Mortality factors	$\bar{X}$% ± S.D.
Dissected Samples (DS) n=379	Mortality of host due to parasitoid	Parasitism (I)	33.12±4.59
		Multi-probing scars, no progeny, host content rotten	1.62±0.78
		Total	34/74±5.41
	Estimated total mortality due to DG		34.74±5.41
			$\bar{X}$% ± S.D.
Reared Samples (RS) n=4201	Total mortality (TM)		42.70±5.61
	Natural mortality		21.45±6.50
	Mortality due to parasitoid (TM-21.45) (II)		21.25±6.71*
	% Parasitoid emergence (no. emerged parasitoid/RS) (III)		19.92±3.67*
	Mortality due to parasitoid besides parasitism (II-III)		1.33±1.40
	Difference of parasitism between DS and RS (I-III)		13.20±5.12

* No significant difference between values with the same marks by t-test, p=0.05.

dissection period. Host feeding is also a possible factor contributing to the mortality of the host which occurred in DG with or without parasitoid progeny. In the present study no attempt was made to quantify the damage done by host feeding.

From the reared samples, the difference between the host mortality due to the parasitoids (II) and the percent of F_1 parasitoid emergence (III) was not significant in BL, TD, or DG. This indicated that parasitism was the major factor causing death of the host species (Tables 10, 12, and 13). Less significant causes of host death could have been repeated probing by BL and DG. Some of the hosts attacked by BL also showed ring-structure damage. A significant difference (II-III) was found in OC (37.5%) (Table 11), which meant some other factor(s) due to the parasitoid beside parasitism was the cause of host death. The dissected samples revealed these factors in OC cases included repeated attacks (5.75%) and a relatively large percentage of ring-structure damage (20.86%). Repeated attacks by BL and DG, as evidenced by multiple scars on the host, by lack of parasitoid progeny, and by decayed host contents were also a minor cause of host death. Ring-structure damage due to OC was identified as one of the major contributing factors to mortality of the host species. Nevertheless, there still remains about 17% (37.51%-20.56%) difference between total mortality and that caused by emerged parasitoids.

The dissected samples revealed the lowest percent parasitism was found in DG (33.12%) (Table 13). This was due to the low number of ovarioles/ovary (n=3) which restricted the number of eggs formed per day (n=6-7). Additionally, occasional superparasitism was observed which

would have restricted the number of host pupae DG could have parasitized on a daily basis.

Overall, BL was responsible for 53% of the mortality of the hosts. OC accounted for 44% of the host mortality. The effectiveness of TD and DG was comparable, since they provided 20.7% and 21.3%, respectively.

Comparisons of Host Associated Olfactory Stimuli

The effects of olfactory stimuli associated with hosts on the parasitoids' host-searching behavior are given in Table 14. The odor of the host fruit or the host itself led the parasitoid to the host. In terms of time of initial response and the vigor of behavior, the attraction of the host odor on the parafilm exposed in the adult fly colony cage for 3 hours was stronger than the odor of the host fruit (Table 14). The strength of the stimuli was related to the number of hosts "surveyed" and/or "probed" within 90 minutes.

The specific factors that attract a parasitoid to its host's environment and enables it to locate the host have been studied extensively. Unlike the results found in this study, parasitoids are often more attracted by their host's food than by the host itself (Read et al. 1970, Wilson et al. 1974). Many parasitoids find hosts by first detecting host indicators such as the frass (Spradbery 1970, Lewis et al. 1976), or materials secreted by the host's mandibular gland during feeding (Calvert 1973, Vinson 1968). In the present study, the bagasse medium, on which host larvae had been fed and which would have held the frass and any material liberated during feeding, elicited no parasitoid response.

From the findings of this study, the attractiveness of the host's odor was responsible for the alteration of the parasitoid's behavior.

Table 14. Comparisons of different olfactory stimuli on host-searching behavior of 3 species of parasitoids.

Observations	Test*	Parasitoid species BL(n=5)	OC(n=5)	TD(n=5)
no. ♀ "surveying" only	A	--	--	--
	B	--	--	--
	C	1	--	--
	D_I	--	--	--
	II	--	--	--
	III	--	--	--
"surveying" + "probing"	A	--	--	--
	B	--	--	--
	C	2	3	4
	D_I	--	--	--
	II	1	1	--
	III	5	5	5
$\bar{X}$ pre-searching time (min) $\bar{X}$±S.E.	C	6±3.2(n=3) (1-12)	36±24.7(n=3) (5-85)	34±15(n=4) (2-60)
	D_{II}	2(n=1)	1(n=1)	--
	D_{III}	1±0.5(n=5) (0.05-3)	2.73±1.82(n=5) (0.7-10)	18.2±10.45(n=5) (1-55)
$\bar{X}$ containers surveyed/♀ $\bar{X}$±S.E.	C	1.67±0.58 a**	1.33±0.58 a	1.5±0.58 a
	D_{II}	4	3	--
	D_{III}	9±2.14 b	5.8±1.65 b	5.6 ± 1.54 b

Table 14--Continued.

Observations	Test*	Parasitoid species		
		BL(n=5)	OC(n=5)	TD(n=5)
$\bar{X}$ containers probed/♀	C	2.0±0 a	1±1 a	1.5±0.58 a
$\bar{X}$±S.E.	D_{II}	3	1	--
	D_{III}	7.4±1.66 b	4.2±1.21 b	4.8±1.2 b

* A: larva only, B: larva + medium, C: guava + larva and parafilm treated with guava juice, D: parafilm exposed in 7-14-day old fly colony cage for different periods of time I: 1 hr, II: 2 hr, III: 3 hr.

** The different letters in the same column within the same observation subject indicate the significant difference by t-test, at p=0.05 (Sokal and Rohlf 1969).

Possibly the attraction provided by A. suspensa males was due to the form of pheromone used to attract virgin females (Nation 1977). Another possibility could be that, as observed in Rhagoletis pomonella (Prokopy and Roitberg 1984) the female, after egg-laying, deposited on the surface of the fruit a trail containing a pheromone that discouraged egg laying. These deposits, therefore, could be used as a kairomone in leading the parasitoid to the host. Also, the effectiveness of the host odor in facilitating host-finding behavior is dependent on its concentration. Thus, these laboratory findings indicate that under field conditions host odor perhaps would be instrumental in leading the parasitoid to the host. The host's odor probably plays a more important role in attracting the parasitoid when the host density is high, and the host's food is probably more important when the density is low.

Determination of "Accepted" Attack

Before parafilm was used in the following behavior studies, it was kept in the adult fly colony cage for at least 3 hours.

Experiments were performed to find indicators of female ovipositor probing versus actual oviposition. The frequency and duration of probing associated with and without egg laying is shown in Table 15. The probing with egg laying took significantly longer than probing without egg laying (Table 15, t-test, $p=0.05$). An overlapping range was found in egg laying and non-egg laying situations in all tested species. Therefore, as mentioned previously, two criteria were used to determine the threshold time for probes which led to egg laying: (1) the majority of successful oviposition should have occurred after the threshold time; (2) the proportion of successful oviposition should have been greater than those of unsuccessful oviposition in a given number of seconds spent by the

Table 15. The duration of probing versus successful oviposition by BL, OC, TD, and DG.

Species		Duration of probing (sec)								$\bar{X}$ ± S.E.
		1-10	11-20	21-30	31-40	41-50	51-60	60-300	301	
BL	eggs laid (n=23)	21.7% (5)	4.3% (1)	8.7% (2)	21.7% (5)	13.0% (3)	17.4% (4)	13.0% (3)	--	41.5±6.71 sec *
	no eggs laid (n=21)	61.9% (13)	14.3% (3)	14.3% (3)	--	9.5% (2)	--	--	--	18.1±4.78 sec
OC	eggs laid (n=14)	--	--	7.1% (1)	7.1% (1)	7.1% (1)	50.0% (7)	28.6% (4)	--	61.43±7.71 sec *
	no eggs laid (n=23)	26.1% (6)	21.7% (5)	21.7% (5)	--	--	17.4% (4)	13.0% (3)	--	30.09±6.47 sec
TD	eggs laid (n=26)	--	11.5% (3)	19.2% (5)	15.4% (4)	7.7% (2)	11.5% (3)	26.9% (7)	7.7% (2)	115.11±7.03 sec *
	no eggs laid (n=32)	62.5% (20)	21.9% (7)	6.3% (2)	3.1% (1)	--	--	6.3% (2)	--	16.69±5.67 sec
DG	eggs laid (n=19)	--	--	--	--	--	--	26.3% (5)	73.7% (14)	16.2±2.11 min *
	no eggs laid (n=17)	5.9% (1)	5.9% (1)	5.9% (1)	5.9% (1)	23.5% (4)	23.5% (4)	23.5% (4)	5.9% (1)	1.74±0.46 min

* Significant difference by t-test at p=0.05.

female probing the host. The second criterion was established to avoid the type II error, the acceptance of a false null hypothesis. Based on these two criteria, the threshold times for egg laying by the four parasitoids was: 31 seconds for BL; 31 seconds for OC; 21 seconds for TD; and 61 seconds for DG. Any "probing" which took longer than or equal to the threshold time was referred to as an "accepted" attack, and that which took less than threshold time was considered as a "rejected" attack. The "rejected" attacks might indicate the existence of host discrimination behavior, since many hymenopterous parasitoids are known to use the insertion of oviposition to distinguish between parasitized and non-parasitized hosts.

Behavioral Observations of Host Discrimination

The different probing behaviors (accepted or rejected) performed by females of different categories (A, B, or rA) under the different conditions (healthy or parasitized hosts) are given in Table 16. The independent test (G-test, Sokal and Rohlf 1969) was applied to determine the interrelationship between the condition of the female and the type of probes performed. An analysis of the results indicates there was no association between the different categories of the female and the probing behavior. All the females of all the studied species exhibited a marked preference for the healthy hosts (Z-test, $p=0.05$; Siegel 1956). The results indicate that all female parasitoids discriminated between parasitized and healthy hosts whether the parasitization was due to the same female or not.

Behavioral studies of the host discrimination abilities of BL and DG reconfirmed the results obtained through statistical analyses (Table 6, Fig. 5). Present findings suggest that TD and OC also exercised host

Table 16. Preference of probing site with healthy or parasitized hosts.

Species	Condition of female†	Number of probes: Into the host "accepted" attacks: healthy host	Into the host "accepted" attacks: parasitized host	Into the host "rejected" attacks: healthy host	Into the host "rejected" attacks: parasitized host	Into the container‡: healthy host	Into the container‡: parasitized host	Total: healthy host	Total: parasitized host
BL	A	28	0	10	3	1	1		
	B	3	0	4	1	1	0		
	rA	4	0	3	1	0	0		
	Total	35	0	17	5	2	1	54	6
	G-test*			G=0.147, NS				**	
OC	A	25	2	8	5	1	1		
	B	8	1	2	1	0	0		
	rA	7	2	2	0	1	1		
	Total	40	5	12	6	2	2	54	13
	G-test			G=0.471, NS				**	
TD	A	8	3	1	2	2	0		
	B	2	0	4	1	0	1		
	rA	8	1	1	0	1	1		
	Total	18	4	6	3	3	2	27	9
	G-test			G=0.803, NS				**	

Table 16--Extended.

DG	A	6	0	2	1	0	0	
	B	7	0	4	1	0	0	
	rA	4	0	1	1	0	0	
	Total	17	0	7	3	0	0	24 - ** - 3
	G-test			G=0.267, NS				

†A: the first introduced female; B: the second introduced female; rA: a reintroduced female.
‡The parasitoid inserted ovipositor through parafilm or on the rim of the container but not into the host.
*G-test is used to test the independence of female conditions and probe preference.
**Significant difference was found by Bionomial analysis (Z-test) at p=0.05.

discrimination. Thus, the egg distribution resulting from either random behavior--as shown by OC--or aggregated behavior--as demonstrated by TD--was probably not due to the failure of host discrimination ability.

The assumption that OC selected hosts for egg laying in a random pattern was rejected after observing that OC showed a preference for healthy hosts for egg laying (Z-test, Table 16). The random egg distribution of OC was probably due to some factor other than random searching behavior. However, unlike BL and DG, OC did not exhibit strict host discrimination and did superparasitize some hosts (Table 16).

The observation of host discrimination behavior by TD seems to conflict with the previous finding that TD needed superparasitization to avoid encapsulation. Possibly TD laid the second egg in the previously parasitized host in a shorter oviposition time. The behavior therefore might have fallen into the category of a "rejected" attack. Thus, the so-called "rejected" parasitized hosts (Table 14) actually were the superparasitized hosts by TD. The female TD may have used a shorter time to lay the second egg because the oviposition site which was drilled during the first oviposition was reused. This conclusion seems improbable, however, because an average of 2.73 (180/66, Table 5) oviposition scars were found per TD progeny as noted in the previous study. Another explanation could be that TD performed host discrimination in a more thorough manner and that the female could detect the number of larvae or eggs which existed in the host and laid the egg in the host containing the least number of eggs (Bakker et al. 1972), as reported in Pseudencoila bochei (Bakker et al. 1972, van Lenteren et al. 1978). This more complex host discrimination behavior might have been overlooked because TD usually took a longer time for the initial response (18±10

minutes, Table 14). It, thus, had a relatively shorter time to fully perform host discrimination within the fixed exposure time (1 hour). However, an average 2.43 eggs per host (Table 6) indicated that some TD parasitoids may have been able to perform the host discrimination ability in this thorough manner.

From the reared samples, in which the individual was kept separately in a gelatin capsule, BL, OC, and DG progeny successfully emerged from the majority of the parasitized hosts (Table 17). The exception was TD, since 50% of the parasitized hosts (11 out of 22) failed to produce TD adults. This low percent of emerged TD was probably due to the fact they were not superparasitized by TD and a high percentage of hosts completely encapsulated the TD larvae.

During the study, a common difficulty was encountered, especially in larval parasitoids, in that the parasitoid rejected many hosts even when they were not parasitized or dead. After the host had been rejected several times it might have been accepted for ovipoisiton at a later host-parasitoid encounter. In the cynipid P. bochei, the variation in percent acceptance of hosts at the first encounter was dependent upon the host's stage of development and the host species (Bakker et al. 1972, Nell et al. 1976). In this study of larval parasitoids, many apparent rejections were not real rejections because positive oviposition was terminated through vigorous activity by the host. The percent acceptance by the hosts at the first host-parasitoid encounter was about 75% in BL, 75% in OC, and 78% in TD (Table 18). Some rejection of DG by host pupae was also observed. The percent acceptance of DG by the host at first host encounter was 81% (Table 18).

Table 17. Number and percentage of parasitoids emerged from different host categories (4 replicates).

Species	No. of parasitoids emerged from "Accepted" hosts	%	"Rejected" hosts	%	Total
BL	31(35)*	88.6%	1(29)	3.4%	32(64)
OC	36(40)	90.0%	0(24)	0%	36(64)
TD	11(18)	61.1%	0(46)	0%	11(64)
DG	17(17)	100%	0(47)	0%	17(64)

*Number in the parenthesis means the total number of pupae observed.

Table 18. Number of hosts rejected and accepted by the parasitoid at the first encounter.

Species	No. accepted	No. rejected	% acceptance
BL	33	13	71.7
OC	29	10	74.4
TD	14	4	77.8
DG	17	4	81.0

Oviposition Restraint Study

As shown in Table 19, when a single parasitoid was isolated at different host densities, the tendency toward superparasitism was stronger in the lower host density (n=5) groups. All four species exercised ovipositional restraint. This was evident since the average egg production per female in the test groups was always lower than in the control group. Unlike BL and DG, there was no significant difference found in the average number of eggs produced per female when different host densities were exposed to a single OC and TD. BL and DG exhibited oviposition restraint by laying significantly fewer eggs as the number of available hosts became smaller. DG was the only species which exercised perfect oviposition restraint. When one female DG was exposed to two or four hosts at a time, with an average less than one egg per host, no superparasitism was found. Within the BL, OC, and TD groups, the average number of eggs per host was higher than one, indicating some failure of oviposition restraint, although females exercised a certain degree of restraint by laying fewer eggs per individual.

When five parasitoids were simultaneously introduced into petri dishes with different host densities, the results showed that superparasitism greatly increased as the number of available hosts became smaller. However, the individual oviposition restraint ability within this group was greater than that of the isolated individual. The average number of eggs laid per female significantly decreased as the number of available hosts decreased. However, the individual restraint shown by these five parasitoid groups might have been greater when superparasitism was significantly increased ($\bar{X}$ eggs/host). The average number of BL, OC,

Table 19. The results of six replicates of oviposition restraint experiment by exposing 1 or 5 females to different host densities for 24 hr.

Species	No. of parasitoids	No. of hosts	N(%) host with n eggs 0	1	≥2	Total no.*	$\bar{X}$ eggs/host $\bar{X}$ ± S.D.	$\bar{X}$ eggs/♀ ** $\bar{X}$ ± S.D.
	1	15	0	47(74)	16(26)	63	1.9±2.0	20.0±1.7 a
		5	0	2(20)	8(80)	10	3.5±2.0	5.8±2.7 b
BL	5	15	0	0	55(100)	55	4.6±2.3	8.4±3.2 a
		5	0	0	10(100)	10	5.8±1.5	1.9±1.3 b
CK(n=3)	1	75	124(61)	78(39)	0	202	0.4±0.5	21.0±3.5
	1	15	11(16)	32(48)	24(36)	67	1.5±2.4	16.7±5.3 a
		5	0	0	20(100)	20	3.6±3.0	12.0±6.6 a
OC	5	15	0	8(11)	68(89)	74	3.0±1.1	7.4±3.1 a
		5	0	4(40)	6(60)	10	4.0±2.3	1.3±0.7 b
CK(n=3)	1	75	58(46)	54(43)	14(11)	126	0.8±1.1	33.3±13.1
	1	15	2(4)	32(58)	21(38)	55	2.4±5.7	22.0±0.7 a
		5	10(63)	2(13)	4(25)	16	5.4±2.0	14.4±3.0 a
TD	5	15	0	3(7)	37(93)	40	14.74±24.7	19.7±18.4 a
		5	2(13)	4(25)	10(63)	16	17.0±12.8	9.1±2.0 b
CK(n=3)	1	75	55(29)	97(51)	37(20)	189	1.1±0.9	67.3±28.0

Table 19--Extended

	1	4	14(58)	10(42)	0	24	0.4±0.5	1.7±1.4	a
		2	8(80)	2(20)	0	10	0.2±0.4	0.3±0.8	b
DG	5	4	0	22(92)	2(8)	24	1.1±0.3	0.9±0.1	a
		2	0	10(83)	2(17)	12	1.2±0.4	0.5±0.1	b
CK(n=3)	1	10	15(50)	15(50)	0	30	0.5±0.5	5.0±2.5	

* Some hosts were rotten before dissection.

** Values in the same column within one experiment followed by the same letter mean no significant difference by t-test, at p=0.05.

TD, and DG eggs found per host was larger than one and much higher than that of the check groups. This indicated that some hosts were excessively superparasitized. Therefore, a failure of restraint was indicated by an increased amount of superparasitism as the parasitoid density increased or the host density decreased.

Excessive superparasitism has been know to weaken the contestants and to produce malformed adults (Salt 1937). However, a large number of the hosts were damaged and could not be dissected. The damage was apparently mainly due to the excessive attacks by the parasitoids because a large number of probing scars were evident on the pupae, and the body content decayed sooner than the decomposition caused by ring-structure or by repeated piercing without laying any eggs. A reduction in the number of eggs laid per female when five parasitoids were present might have been caused by mutual interference. As some 'O-groups' remained non-parasitized, it appeared that a female did not search all the non-parasitized hosts before she superparasitized some.

The smallest amount of superparasitism was found in DG parasitized hosts, with an average of about one egg per host when five parasitoids were exposed (Table 19). This indicated DG exercised oviposition restraint. This ability may have compensated for the small number of eggs produced daily by DG and the greater amount of time and energy it needed for each oviposition ($\bar{X}$=16.2 min, Table 15).

The superparasitism of BL, OC, and TD found in the study on egg distribution might have been partially due to the failure of oviposition restraint when the number of parasitized hosts increased.

Mutual Interference Among Searching Adults

The female searching pattern of BL has been described by Lawrence (1981b), and a similar searching pattern has also been reported in TD (Nunez-Bueno 1982). This study revealed the host searching patterns of OC and DG are similar to that of BL or TD. The common searching pattern was as follows:

(1) Walking - the female approached a host, and landed upon it;

(2) Resting - the antennae alternately tapped on the surface;

(3) Probing - the female raised up her ovipositor and pierced the host;

(4) Resting - after the female withdrew her ovipositor, she remained at the same spot to "clean" the antennae or ovipositor.

There are some differences in behavior among the four species after the fourth step. After the resting activity described in the fourth step, usually OC and BL walked away from the area and approached another host or revisited the same host. At this step, the female TD and DG parasitoids usually performed a number of turning or circling movements around the host. These circling movements only occasionally occurred in BL or OC after the fourth step, and they were more consistently observed in DG than in TD. DG also demostatrated the movements between the walking and resting stages described in the first and second steps. Therefore, in light of this finding, the circling movements shown by DG could be considered a host discrimination as well as a marking behavior.

Sometimes DG was also found to apply an exudate on the host from the tip of the ovipositor after the female withdrew her ovipositor. The function of this oil-like exudate is unknown. It probably serves as a

"marking" material (Rabb and Bradley 1970). The source of the exudate may be from the Dufor's gland as reported in Cardiochiles nigriceps Vierick by Vinson (1969). Usually DG applied an exudate to the host before the host feeding took place. This application of exudate caused some doubt as to the exact nature of the host-feeding behavior, since it was uncertain as to whether DG was feeding on the host or the exudate. However, under laboratory conditions, the application of exudate by DG was not performed on a regular basis. Sometimes the female applied it after a "rejected" attack (no egg-laying probe). If the exudate was used as a marking material this behavior may have resulted in the waste of potential hosts.

The regular searching pattern was subject to change due to the different degrees of interference competition. The interference ("contact") among searching adults resulted in a disruption of their normal pattern, i.e. their behavior was either discontinued, changed, or sometimes remained normal after the interruption.

Experiment I: Parasitization in Confined Host Densities

The density dependent relationship was demonstrated between total mortality and host density as well as between the percent F_1 parasitoid emergence and host density was demonstrated by the positive regression coefficient (b) (Table 20). In BL, OC, and TD, these density-dependent relationships became somewhat stronger when the number of parasitoids increased. These increments were demonstrated by the increasing steepness of the slopes (b). In DG where the inverse density-dependent relationship was noted, the decline occurred because the great host density was beyond DG's reproductive capacity.

Table 20. The responses of host mortality and F_1 parasitoid emergence of BL, OC, TD and DG to a fixed host density.

No. Parasitoid	BL	OC	TD	DG
		% Total host mortality		
1	y=91.70 - 0.07x	y=70.81 + 0.08x	y=78.76 - 0.18x	y=60.06 - 0.69x
2	y=93.57 - 0.19x	y=56.49 + 0.59x	y=89.58 - 0.49x	y=90.55 - 1.09x
4	y=99.48 - 0.02x	y=100 + 0x	y=86.47 - 0.16x	y=102.14 - 1.06x
		% Parasitoid emerged (F_1)		
1	y=8.46 + 0.26x	y=2.66 + 0.01x	y=1.43 + 0.26x	y=38.61 - 0.53x
2	y=7.19 + 0.12 x	y=1.71 + 0.04x	y=5.24 + 0.01x	y=55.01 - 0.86x
4	y=5.15 + 0.25x	y=0.17 + 0.07x	y=1.90 + 0.30x	y=53.34 - 0.77x

To determine the response of parasitoids to host density, the average searching efficiency of an individual parasitoid was measured. The area of discovery (a) was used to measure the individual searching efficiency when the parasitoid density (p) varied, and the formula was:

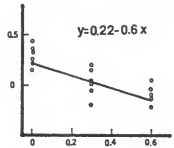
$$a = \frac{1}{p} \log_e \frac{Ub}{Us},$$

where Ub was the initial host density and Us represented the number of hosts surviving after exposure to the parasitoids (Nicholson 1933). The average searching efficiency of the individual, expressed as log a, rose as the parasitoid density (log p) fell, resulting in an inverse density-dependent relationship between them (Fig. 6). This is a classic mutual interference relationship which also has been demonstrated by Hassell (1971a,b) and Ridout (1981). This inverse density-dependent relationship indicated that there was some density-dependent factor influencing the adult parasitoid population. This relationship was stronger than the relationship between the responses of the parasitoid (total mortality of host) and host density. Therefore, searching efficiency was more sensitive to the parasitoid to host ratio than was host mortality. When the parasitoid number was doubled, the slopes representing these inverse density-dependent relationships were larger than the differences between the slopes representing host density-dependent relationships. The encounters between adult parasitoids have a major impact on host-parasitoid relationships and individual parasitoid searching efficiency.

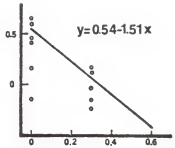
The extent of the change in the behavior of the parasitoids upon encountering other parasitoids varied by species (Tables 21-24). When encounters took place during probing and resting, the parasitoid usually changed its behavior pattern to walking; therefore, probing and resting

Fig. 6. Relationship between log area of discovery (log a) and log parasitoid density when the parasitoids were confined with a fixed host density each time.

Log Area of Discovery

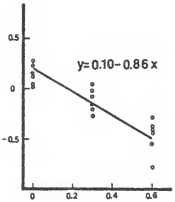


B. longicaudatus

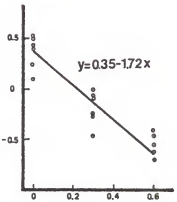


O. concolor

T. daci



D. giffardii



Log Parasitoid Density

Table 21. The behavior pattern of BL after encounters with other BL.

Encounter during	Behavior pattern after encounter			Total encounters (%)
	Walking (%)	Resting (%)	Probing (%)	
Walking	83 (60)	51 (37)	5 (3)	139 (100)
Resting	10 (71)	4 (29)	--	14 (100)
Probing	27 (64)	2 (5)	13 (31)	42 (100)
				195

% of behavior change upon encounter = 49%

Table 22. The behavior pattern of OC after encounters with other OC.

Encounter during	Behavior pattern after encounter			Total encounters (%)
	Walking (%)	Resting (%)	Probing (%)	
Walking	18 (100)	--	--	18 (100)
Resting	12 (86)	2 (14)	--	14 (100)
Probing	1 (20)	2 (40)	2 (40)	5 (100)
				37

% of behavior change upon encounter = 41%

Table 23. The behavior pattern of TD after encounters with other TD.

Encounter during	Behavior pattern after encounter			Total encounters (%)
	Walking (%)	Resting (%)	Probing (%)	
Walking	91 (96)	5 (4)	--	96 (100)
Resting	37 (74)	10 (20)	2 (6)	50 (100)
Probing	6 (13)	4 (9)	36 (78)	46 (100)
				192

% of behavior change upon encounter = 29%

Table 24. The behavior pattern of DG after encounters with other DG.

Encounter during	Behavior pattern after encounter			Total encounters (%)
	Walking (%)	Resting (%)	Probing (%)	
Walking	19 (100)	--	--	19 (100)
Resting	1 (20)	4 (80)	--	5 (100)
Probing	1 (4)	1 (4)	22 (92)	24 (100)
				48

% of behavior change upon encounter = 6%

times decreased and walking time increased. The decreased probing time was compensated for by increased walking time, since the increased walking extended the time spent searching for more hosts. When encounters took place during walking, usually the parasitoid continued walking.

In BL (Table 21), the overall behavior change upon meeting another parasitoid was 49%. When encounters took place during probing, 64% of the BL parasitoids would stop probing and begin walking. Sixty percent of the walking activity would continue after encounters, and 71% of the resting activity would change to walking upon meeting another. OC and TD (Tables 21 and 23) demonstrated a similar behavior change pattern after encounters although the percentages of behavior change were smaller than that shown by BL. OC exhibited 41% and TD showed 29% of behavior change upon encounters. DG (Table 24) demonstrated the least behavior change upon encounters (6%), thus 94% would remain in the same behavior mode after an encounter.

The effects of host density on behavior responses by each species at various parasitoid densities are given in Tables 25-28. Typically, the time spent on each contact was very short, usually less than 1 second. As soon as the DG or OC parasitoids encountered each other, both immediately changed behavior and/or one moved away. Therefore, the percentage of time spent in contact by these parasitoids was too trivial to be measured. In contrast, each contact by TD lasted from 4 to 110 seconds. Encounters between BL parasitoids lasted from 1 to 13 seconds.

In OC very few contacts were observed in four-parasitoid situations, and no contact was found in two-parasitoid situations. From behavioral

Table 25. The behavioral responses of TD to a fixed density of A. suspensa and the correlation between various activities.

	1 parasitoid	2 parasitoids	4 parasitoids
% walking	y=53.72+0.58x, r=0.73	y=60.44+0.58x, r=0.73	y=82.77-0.71x, r=0.85
% probing	y=15.46+0.17x, r=0.38	y=1.45+0.32x, r=0.98*	y=11.57+0.38x, r=0.90*
% resting	y=34.39-0.75x, r=0.85	y=14.64+0.36x, r=0.53	y=11.28+0.40x, r=0.73
No. probes	y=2.23+0.14x, r=0.68	y=1.65+0.06x, r=0.80	y=-0.09+0.24x, r=0.98*
% contact		y=0.08+0.002x, r=0.15	y=3.45-0.07x, r=0.42
No. contacts		y=0.89+0.01x, r=0.18	y=2.14-0.01x, r=0.34
$\bar{x}$ sec/probe	y=71.17-1.04x, r=0.35	y=39.7-0.52x, r=0.59	y=23.38-0.26x, r-0.41
$\bar{x}$ sec/contact		y=1.50+0.02x, r=0.11	y=22.80-0.30x, r=0.30
	Coefficient of correlation (r) between activities		
% walking vs % resting	r=-0.9*	r=-0.9*	r=-1*
% resting vs % probing	r=0.3	r=0.8*	r=1*
% walking vs % probing	r=-0.6	r=-0.9*	r=-1*
% walking vs no. contacts		r=-0.63	r=0.58

Table 25--Extended.

% probing vs no. contacts		r=0.43	r=-0.50
No. probes vs no. contacts		r=0.58	r=-0.53
% resting vs no. contacts		r=0.9*	r=-0.5
No. probes vs $\bar{x}$ sec/probe	r=-0.4	r=0.2	r=1*
No. contacts vs $\bar{x}$ sec/contact		r=0.93*	r=0.43
No. probes vs % resting	r=-0.5	r=0.7*	r=1*
No. probes vs % probing	r=0.3	r=0.7*	r=1*

*Significant correlation at p=0.05.

Table 26. The behavioral responses of DG to a fixed density of A. suspensa and the correlation between various activities.

	1 parasitoid	2 parasitoids	4 parasitoids
% walking	y=12.95+0.06x, r=0.1	y=65-0.37x, r=0.3	y=46.66+0.10x, r=0.5
% resting	y=67.25-0.06x, r=0.4	y=27.24+0.41x, r=0.4	y=41.95-0.719x, r=0.93
% probing	y=19.7-0.06x, r=0.14	y=14.81-0.45x, r=0.17	y=8.87+0.67x, r=0.88
% circling	y=0.15+0.05x, r=0.92*	y=0.42+0.01x, r=0.23	y=1.80-0.03x, r=0.33
No. probes	y=0.29+0.003x, r=0.17	y=0.32+0.024x, r=0.67	y=1.02+0.04x, r=0.8
No. circlings	y=0.45+0.024x, r=0.94*	y=0.39+0.01x, r=0.83	y=0.74+0.032x, r=0.79
No. contacts		y=0.45+0.005x, r=0.24	y=1.80+0.024x, r=0.61
$\bar{x}$ sec/probe	y=271.3-2.33x, r=0.5	y=195.02-3.72x, r=0.54	y=91.75+1.42x, r=0.71
	Coefficient of correlation (r) between activities		
% walking vs % resting	r=-0.7*	r=-1*	r=-0.8*
% resting vs % probing	r=0.1	r=0.68	r=0.6
% walking vs % probing	r=-0.4	r=-0.63	r=-0.7*
% circling vs % probing	r=0.2	r=-0.1	r=-0.1

Table 26--Extended.

No. probes vs no. circlings	r=0.5	r=0.83*	r=0.9*
No. probes vs no. contacts		r=0.48	r=-0.9*
% probing vs no. contacts		r=-0.8*	r=-1*
% resting vs no. contacts		r=0.48	r=0.6
% walking vs no. contacts		r=-0.43	r=0.7*
No. circlings vs % circling	r=1*	r=-0.33	r=0.9*
No. circlings vs % walking	r=0.6	r=-0.18*	r=-0.7*
No. probes vs % probing	r=0.9*	r=0.68	r=0.7*
No. probes vs $\bar{x}$ sec/probe	r=0.5	r=-0.5	r=0.9*
% probing vs $\bar{x}$ sec/probe	r=0.7*	r=0.4	r=0.7*
No. contacts vs no. circlings		r=0.63	r=-0.9*

*Significant correlation at p=0.05.

Table 27. The behavioral responses of BL to a fixed density of A. suspensa and the correlation between various activities.

	1 parasitoid	2 parasitoids	4 parasitoids
% walking	y=36.06+0.31x, r=0.66	y=48.70-0.53x, r=0.32	y=27.43+0.19x, r=0.25
% probing	y=15.53+0.26x, r=0.37	y=4.92+0.06x, r=0.20	y=11.19+0.20x, r=0.56
% resting	y=48.42-0.57x, r=0.63	y=53.24+0.10x, r=0.06	y=60.52-0.39x, r=0.37
No. probes	y=3.89+0.09x, r=0.54	y=0.72+0.03x, r=0.46	y=3.81-0.18x, r=0.18
% contact		y=0.06-0.001x, r=0.45	y=-0.17+0.02x, r=0.89*
No. contacts		y=0.51-0.01x, r=0.43	y=0.63+0.04x, r=0.13
$\bar{x}$ sec/probe	y=57.26-0.68x, r=0.94*	y=30.33+0.02x, r=0.02	y=24.2-0.18x, r=0.62

	Coefficient of correlation (r) between various activities		
% walking vs % resting	r=-0.6	r=-1*	r=-0.9*
% resting vs % probing	r=-0.9*	r=-0.7*	r=-0.7*
% walking vs % probing	r=0.3	r=0.7*	r=0.6
% walking vs no. contacts		r=0.85*	r=0.6

Table 27--Extended.

No. probes vs no. contacts		r=0.1	r=0.6
No. probes vs $\bar{x}$ sec/probe	r=-0.8*	r=0.1	r=-0.8*
% resting vs no. contacts		r=-0.7*	r=-0.7*
No. probes vs % probing	r=0.5	r=0.7*	r=-0.6

*Significant correlation at p=0.05.

Table 28. The behavioral responses of OC to a fixed density of A. suspensa and the correlation between various activities.

	1 parasitoid	2 parasitoids	4 parasitoids
% walking	y=5.5+0.16x, r=0.37	y=11.94+0.002x, r=0.004	y=8.44+0.64x, r=0.81*
% probing	y=0.028+0.22x, r=0.57	y=3.42+0.16x, r=0.58	y=2.58+0.16x, r=0.39
% resting	y=95.49-0.48x, r=0.63	y=84.67-0.16x, r=0.23	y=87.02-0.80x, r=0.96
No. probes	y=1.89+0.04x, r=0.58	y=1.22+0.016x, r=0.29	y=4.60-0.14x, r=0.98*
$\bar{x}$ sec/probe	y=7.67+0.62x, r=0.58	y=19.95+0.73x, r=0.62	y=11.5-2.25x, r=0.32
No. contacts			y=-0.34+0.04x, r=0.02
	Coefficient of correlation (r) between activities		
% walking vs % resting	r=-0.8*	r=-0.9*	r=-0.9*
% resting vs % probing	r=-0.9*	r=-0.4	r=-0.2
% walking vs % probing	r=0.9*	r=0.3	r=-0.1
No. probes vs $\bar{x}$ sec/probe	r=1*	r=0.23	r=0.3
No. probes vs % probing	r=1*	r=0.83*	r=0.4
No. contacts vs % walking			r=0.8*
No. contacts vs no. probes			r=0.8*

*Significant correlation at p=0.05.

observations, the small number of contacts was probably due to the fact that the OC parasitoid tended to restrict its movements to a more local vicinity (with or without hosts) and seldom extended its movement beyond that area. This relatively localized movement might have been the indirect cause of superparasitism. The direct cause would be the failure of oviposition restraint, since only a limited number of hosts were present within the localized range.

When the numbers of the parasitoids increased, TD was the only species in which the density-dependent relationship between host density and percent of time probing became stronger and more significant (Table 25). In most TD cases, the behavior pattern did not change upon encounter. Therefore, the percent of time walking, resting, and probing was not effected by the number of contacts between adults. There was no significant correlation between the above activities and the number of contacts. There was, however, a significant correlation between percent of time probing and number of probes. A significant correlation was observed in the two-parasitoid situation between the percent of time resting and the number of contacts. When encounters occured during probing, the female sometimes withdrew the ovipositor and started antennal or ovipositor cleaning. Then the female reinserted the ovipositor into the host. Therefore, both the percent of time resting and the percent of time probing increased with the number of contacts. Conversely, the percent of time walking decreased as the number of encounters rose.

DG (Table 26) was the only species which showed the inverse density-dependent relationship between the percent of time probing and host density when one and two parasitoids were present. This is again

because of the DG parasitoid's tendency to spend a long time probing and its low reproductive capacity. The long time spent probing might be a factor that contributes to low reproductive capacity. When four parasitoids were present, the percent of time probing became density dependent. DG was the species which demonstrated the least behavior change following encounters (Table 24). But DG had the tendency to prolong the phase of search behavior exhibited at the time of an encounter. In four-parasitoid situations, most encounters took place during walking. Thus, the percent of time walking and the number of contacts were significantly correlated (r=0.7). As a result, DG spent less of its time probing and resting. The number of probes by DG, however, were reduced due to the increased contacts with other parasitoids (r=-0.9). The encounters in two-parasitoid situations took place during resting, but the number of encounters were too few to draw any conclusions about DG's behavior patterns. It can also be noted that in DG the number of circling movements was significantly and also positively correlated with the number of probes. Therefore, the circling movement can be assumed to be "marking" and/or "surveying" functions. The circling movements took place more often after probing than before probing. When the parasitoid density increased, this type of correlation became stronger (r=0.5 to r=0.9). This indicated that when DG parasitoids aggregated, individuals had a stronger tendency to mark or survey the probing site in order to avoid superparasitism. In most cases the percent of time circling and number of circlings had a significant positive correlation.

In BL and OC (Tables 27 and 28) the percent of time resting was negatively associated with the percent of time probing, and the

relationship between the number of probes and the percent of time probing became negatively correlated as the number of parasitoids increased. In BL, this inverse correlation was due to the increasing number of contacts which took place during probing or resting. Thus, those contacts would change the BL's behavior to walking. Therefore, percent of time walking was positively correlated with the number of contacts. The extended walking led BL in search for more hosts and then probing behavior. As a result, the number of probes was positively associated with the number of contacts. The relationship between number of probes and the percent of time probing was not necessarily stable, since encounters sometimes caused the cessation of a probing activity but resulted in a greater number of probes.

In OC, the density-dependent relationship between the percent of time spent probing and host density lasted as long as the number of parasitoids increased. The relationship was less strong when only one parasitoid was present (b=0.16 vs. b=0.22). OC was the least aggressive of the species studied and spent the most time resting. As a result, the number ot contacts by OC were relatively few. No contact was observed in the entire two-parasitoid experiment. The number of probes vs. the percent of time probing had a strong positive correlation until some encounters which occurred in the four-parasitoid situations were considered. In the four-parasitoid situations, the encounters during walking did not change the OC parasitoid's behavior pattern. Therefore, as the percent of time walking increased this led to a larger number of probes but not to an increase in the average time per probe or total percent of time probing.

Table 29. The responses of total host mortality, F_1 parasitoid emergence, and sex ratio of different tested species to various parasitoid and host ratios. Parasitoids were confined with a fixed host density each time.

No.	No.	BL			OC			TD			DG		
parasitoid	host	$\bar{x}$ H.D.(%)[a]	$\bar{x}$ para.(%)[b]	♂/♀	$\bar{x}$ H.D.(%)	$\bar{x}$ para.(%)	♂/♀	$\bar{x}$ H.D.(%)	$\bar{x}$ para.(%)	♂/♀	$\bar{x}$ H.D.(%)	$\bar{x}$ para.(%)	♂/♀
1	3	3.0(100)	0	--	2.6(87)	0	--	2.4(80)	0	--	1.7(56)	1.0(33)	1♂
	6	4.7(74)	0.7(11.7)	1.33	4.0(67)	0.3(5)	1♀	4.3(72)	0	--	3.7(62)	3.0(50)	1.25
	12	11.0(92)	3.0(25)	1.20	10.1(83)	0	--	10.0(83)	0.7(6)	1.0	6.7(56)	4.7(39)	1.8
	24	18.7(78)	2.0(8.3)	0.90	13.4(56)	1.7(7)	0.67	18.0(75)	3.7(15)	0.57	8.0(33)	3.3(14)	1.5
	48	42.7(84)	9.7(20)	0.80	38.0(80)	0.7(1.5)	2♂	33(68)	5.0(10)	0.50	14.7(31)	7.7(16)	1.1
2	3	2.0(67)	0	--	1.7(57)	0	--	3.0(100)	0	--	2.6(86)	1.3(43)	4♂
	6	6.0(100)	0	--	4.3(72)	0	--	5.0(83)	0.3(5)	1♂	5.6(93)	3.3(55)	1.5
	12	11.6(97)	3.3(28)	2.33	10.0(83)	1.0(8.3)	3♀	7.3(61)	1.3(11)	4♀	8.3(69)	6.0(50)	1.6
	24	19.0(80)	2.3(10)	1.33	13.3(55)	0		20.0(84)	1.3(5.5)	4♀	15.0(62)	7.7(32)	1.8
	48	36.0(75)	4.7(10)	1.80	41.7(87)	1.7(3.5)	4.0	31.0(64)	2.0(4)	0.50	18.0(38)	3.7(8)	0.6
4	3	3.0(100)	0	1♀	3.0(100)	0	--	2.7(90)	0	--	1.7(56)	0.7(23)	2♀
	6	6.0(100)	0	--	6.0(100)	0	--	4.7(78)	0	--	5.6(93)	3.3(55)	0.43
	12	12.0(100)	1.7(14)	1.5	12.0(100)	0	--	10.7(89)	0.7(6)	2♂	11.0(92)	8.7(73)	2.25
	24	21.7(90)	1.0(4)	0.5	21.0(87)	1.0(4)	0.5	19.0(79)	5.0(21)	0.36	17.6(73)	11.3(47)	1.41
	48	47.0(98)	10.0(21)	0.25	48(100)	1.0(2)	2.0	37.6(78)	5.3(11)	1.25	25.3(53)	14.3(30)	1.15

[a] $\bar{x}$ H.D.: Average number of host deaths.

[b] $\bar{x}$ para.: Average number of F_1 parasitoid emerged.

The percentage of F_1 parasitoid emergence and progeny sex ratio as affected by changes in the parasitoid to host ratio are shown in Table 29. Generally, the number of F_1 progeny per female increased as host density increased and decreased as the parasitoid density increased. The higher the parasitoid to host ratio (P:H) the more extreme the superparasitism and/or mutual interference; therefore, the smaller the number of F_1 parasitoid progeny. In some extremely competitive situations, few or no progeny emerged (P:H=1:3, 1:6, 2:3, 2:6, 4:3, 4:6). The majority of dead pupae from the BL groups were found with multiple probing scars indicating that mortality was attributed to multiple piercing. With the exception of a few in the P:H=1:24, 1:48, 2:24, and 2:48, the main cause of mortality of unhatched pupae in the OC groups was ring-structure damage. As was noted in Chapter III, no egg laying was involved in the ring-structure damaged hosts. The female tended to kill the host and thus would inhibit other females from laying eggs on the dead host. When the parasitoid density was as high as four, the ring-structure damage was found on every dead pupa. If the ring-structure was attributed to an OC behavior rather than a host response to OC, then it can be considered a manner of host destruction which is a predacious rather than a parasitic behavior. Therefore, OC females exhibited a predacious behavior when the host density was low or P:H was high and became more parasitic when host density was higher or P:H was lower. However, the total mortality of OC groups was comparable to that of BL groups.

In the DG group, the percent of F_1 parasitoid emergence declined when the P:H became 1:6 (1:6, 2:12, 4:24) or lower. The decline was due to the fact that maximum reproductive capacity of DG was six or

occasionally seven progeny/female/day. Thus any P:H lower than 1:6 would result in a waste of hosts. As previously stated, parasitism was the major host mortality factor caused by DG; therefore, the percent of total mortality followed the same trend as the percent of emerged parasitoids.

Compared to BL and DG groups, a smaller number of TD parasitoids emerged. This might have been due to encapsulation which killed the parasitoids. The high percent of hosts killed might be due to the large number of capsules, or to the damage caused by multiple probes in extremely competitive situations (P:H=1:3, 1:6, 1:12, 2:3, 4:3, 4:6, 4:12).

The examination of progeny sex ratio revealed that the number of female progeny tended to increase as the P:H decreased, except in the P:H=4:3 and 4:6 groups of the DG and OC groups. Because of the small number of parasitoids which successfully emerged, the OC groups revealed no obvious pattern of progeny sex ratios.

The general pattern of sex ratio changes might be explained in the following manner. First, females fertilized relatively fewer eggs at high P:H ratios, thus more female-biased sex ratios were found at low P:H ratios (Wylie 1966). Second, the parasitoid contamination increased as the P:H ratio increased (Legner 1967). The parasitoid contamination took place when the parasitoids which touched, or probed into a host without oviposition, rendered that host a less suitable repository for the fertilized egg of another parasitoid (Legner 1967).

Two possible reasons for females fertilizing relatively fewer eggs at high P:H ratios were discussed by Wylie (1966) based on the research on Nasonia vitripennis (Walk.), the pupal parasitoid of the housefly. First, when parasitoids encounter relatively more previously attacked

hosts, they lay a smaller percent of fertilized eggs, though the reason for this change in behavior is not known. Second, the parasitoid more often encounters other female parasitoids while ovipositing, and this interference may reduce the percentage of fertilized eggs laid. The latter possibility might be the case in BL since the probing behavior always changed to another behavior after encounters between adults.

In BL, when egg fertilization is reduced, the wastage of immature parasitoids might be less than in some species, since BL males are smaller than females and thus need less food to mature (Lawrence et al. 1978, Lawrence 1981a). In OC, TD, and DG further study of size differences is needed. Observations by the naked eye, however, revealed that the male and female OC, TD, and DG are more similar in size than the male and female BL.

Evolutionally, the increase in the number of males in an extremely competitive situation will provide greater assurance of mating when host populations are low (Wilkes 1963, Werren 1980). However, in the DG group during times of each extreme competition, for example as P:H=4.:3 and 4:6, the number of females increased. A similar phenomena was observed in Caraphractus (Jackson 1966). Therefore the sex ratio produced by individual females should be further examined to determine whether they definitely lay male and female eggs in a given, genetically-determined, ratio.

Experiment II: Parasitization in Open Choice Host Densities

The density-dependent response of total mortality by BL, TD, and DG on host density was demonstrated again in the open choice experiment. The greater slopes (b) indicated the relation was stronger than that in the fixed density experiment (Table 30). Thus, these parasitoids

Table 30. The responses of host mortality and F_1 parasitoids emergence of BL, OC, TD, and DG to an open choice of their host densities.

No. parasitoids	% Host mortality			
	BC	OC	TD	DG
1	y=48.71+0.38x, r=0.49	y=56.78+0.03x, r=0.04	y=50.73+0.38x, r=0.33	y=59.60+0.20x, r=0.25
4	y=63.53+0.08x, r=0.11	y=65.44-0.57x, r=0.68	y=42.91+0.55x, r=0.33	y=41.92+0.27x, r=0.63
16	y=85.14+0.23x, r=0.85	y=74.48+0.08x, r=0.11	y=57.28+0.02x, r=0.06	y=71.11+0.12x, r=0.26
	% F_1 parasitoids emerged			
1	y=8.31-0.19x, r=0.62		y=3.94-0.009x, r=0.47	y=11.94-0.17x, r=0.3
4	y=2.78+0.12x, r=0.80	y=2.42-0.04x, r=0.30	y=2.65+0.02x, r=0.11	y=-1.04+0.20x, r=0.96
16	y=17.37+0.06x, r=0.01	y=0.07+0.03x, r=0.61	y=10.27-0.16x, r=0.95	y=42.13-0.11x, r=0.21

appeared to satisfy the definition of a density-dependent mortality factor (van den Bosch and Messenger 1973), i.e. the higher the host density, the greater the percentage of hosts killed, therefore the parasitoids are capable of stablizing the host numbers. In the open choice experiment, parasitoids attempted to aggregate where the host density was high (Table 31). OC was the least aggressive of the four species studied, and it had an unstable relationship with host density in the open choice experiment. This might have been due to chance selection of a host population. Once it randomly chose a host density to land on, OC started its localized movement and stayed at that same host density for quite a while.

Unlike the fixed density study, in the open choice experiment the percent of F_1 parasitoid emergence did not always show a density-dependent relationship. This was because the highest level of competition was switched from low host density to high host density in the open choice experiment. The greater slopes (b) for most species indicated the inverse density-dependent relationship between log a and log p became stronger than that in the fixed density environment (Fig. 7).

During searching, the female tapped the surface and tested the subject with her ovipositor, hence, "searching" and "probing" were considered similar behaviors. But the time spent probing was not directly related to searching efficiency, since the searching efficiency fell while the percent of time spent probing did not (Fig. 8). These results were different from Hassell's (1971a,b) observations on Venturia (=Nemeritis) canescens in which the percent of searching (i.e., probing) time and searching efficiency fell at corresponding rates. The present results agreed with Ridout's (1981) findings on Venturia (=Nemeritis)

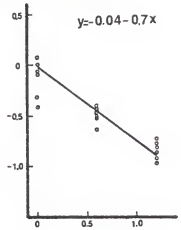
Table 31. Percentage of time spent on 5 host densities allocated to various activities of individual females of 4 species at 3 densities.

Species	No. female	% time spent by female at indicated host density						% time each female spent				
		3	6	12	24	48	transit*	probing	walking	resting	circling	contact
BL	1	16.2	--	16.2	--	--	67.6	2.78	27.91	69.22	--	--**
	4	12.5	--	--	12.4	11.7	73.4	11.31	34.98	52.65	--	--
	16	--	13.0	28.6	12.7	36.1	9.6	37.30	33.00	29.08	--	0.02
OC	1	--	--	--	--	--	100	--	57.78	42.22	--	--
	4	--	--	--	--	--	100	--	33.55	66.34	--	0.11
	16	22.0	21.0	--	--	3.7	56.3	16.70	18.72	63.14	--	--
TD	1	--	--	--	--	54.0	46.0	7.08	65.15	22.78	--	--
	4	--	--	7.0	5.9	67.2	19.9	24.69	52.01	22.66	--	0.83
	16	22.0	--	18.5	24.5	19.0	16.0	22.62	65.90	9.42	--	2.19
BG	1	--	--	19.0	--	--	81.0	12.22	67.00	20.00	0.67	--
	4	--	26.5	--	35.9	9.0	28.6	28.38	58.46	12.12	1.01	--
	16	7.9	7.9	15.3	8.2	47.5	13.4	42.86	44.25	11.67	1.13	--

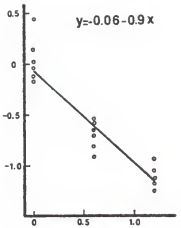
* Transit means the time spent outside the ring units or petri dishes.
** Contact time in most cases was too trivial to be measured.

Fig. 7. Relationship between log area of discovery (log a) and log parasitoid density when the parasitoids were provided an open choice of host density.

Log Area of Discovery

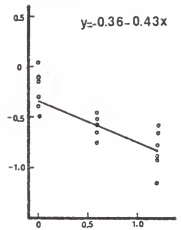


B. longicaudatus

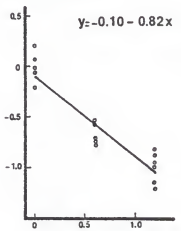


O. concolor

T. daci

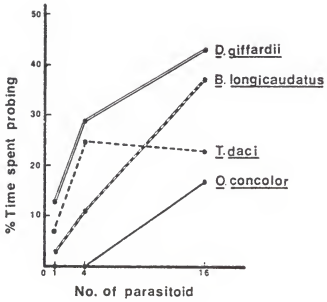


D. giffardii



Log Parasitoid Density

Fig. 8. Relationship between percentage of time spent probing and parasitoid density.


50
40
30
20
10
% Time spent probing
0
1
4
16
No. of parasitoid
D. giffardii
B. longicaudatus
T. daci
O. concolor

canescens which showed that the percent of searching time did not fall as Hassell indicated.

The "false" probing time and the reduced searching efficiency may have had several causes. Host discrimination behavior in which the insect inserted its ovipositor in the host reduced searching efficiency by reducing the time available for "true" probing. When encapsulated, the parasitoid progeny usually died. The host, however, could have survived with three to four capsules. This could have been responsible for an "apparent" decreased searching efficiency. Similar findings were discovered for Venturia (=Nemeritis) canescens which was encapsulated by Ephestia cautella. Rogers (1972) determined encapsulation was responsible for a reduction in searching efficiency. Searching efficiency was also limited by the superparasitism demonstrated by all four parasitoids. Because of superparasitism, time was lost when the parasitoids probed previously attacked hosts. Additionally, vigorous movements by the hosts that were successful in repelling the parasitoids--even if only temporarily--reduced searching efficiency. The efficiency of a parasitoid's searching behavior was affected, too, by the interference created by encountering another parasitoid. Such encounters often caused incomplete oviposition. As a result, time was wasted on incomplete probing.

As mentioned earlier, on the average, a greater number of F_1 parasitoids emerged from high host density groups. This number increased as the number of female parasitoids increased. Total mortality was lower in the open choice studies than in the fixed density groups. This indicated that the parasitoids in the open choice study had a tendency to choose the higher host densities. When only one OC was present, few or

no parasitoids emerged. This most likely indicated an inability by the OC parasitoids to detect the host's existence in the relatively larger (38 x 34 x 20 cm) environment. Compared to those in the fixed density studies, fewer ring-structure damaged hosts were found. But in some high P:H cases (1:3, 4:3, 4:6, 16:6), almost all the dead pupae showed ring-structure damage. This was because when female parasitoids accidentally landed on the sting units with lower host density, the insect had a tendency to localize its movements. The female then performed more predacious behavior than parasitization.

The most contradictory finding was the difference between the progeny sex ratios exhibited in the open choice experiments as compared to those shown in the fixed density experiments. In the open choice experiment, the male-biased sex ratio had a general tendency to increase as the P:H ratio decreased (Table 32). This might have been because parasitoids tended to prefer areas with high host densities. Competition in those environments was therefore more intense. The male parasitoid typically predominated when competition was extreme. However, when host density was low--and as a result, competition was limited--the female predominated.

Other factors, such as host size (Clausen 1939, Rechav 1978, Lawrence 1981b) or environmental conditions, including day length and temperature (Flanders 1947, 1956), have been known to influence the progeny sex ratio. However, since these factors are difficult to control, in attempts to establish a field colony it would seem advantageous to use a small number of parasitoids at any given site. The limited competition and contamination in the area would then favor female progeny production.

Table 32. Responses of host mortality, F_1 parasitoids emergence, and sex ratio of 4 tested species at at 3 densities.

No. parasitoid	No. host	EL			OC			TD			DG		
		$\bar{x}$ H.D.(%)[a]	$\bar{x}$ para.(%)[b]	♂/♀	$\bar{x}$ H.D.(%)	$\bar{x}$ para.(%)	♂/♀	$\bar{x}$ H.D.(%)	$\bar{x}$ para.(%)	♂/♀	$\bar{x}$ H.D.(%)	$\bar{x}$ para.(%)	♂/♀
1	3	1.0(33)	0.3(10)	1	2.3(77)	0	--	0.7(23)	0	--	1.3(43)	0	--
	6	3.6(60)	0.3(5)	1	3.0(50)	0	--	2.0(31)	0.3(5)	1	3.6(60)	1.3(22)	4
	12	5.5(46)	0	--	7.5(61)	0	--	4.3(36)	0.3(2.5)	1	8.3(69)	1.0(8.3)	2.0
	24	14.8(62)	0	--	16.0(67)	0	--	6.8(28)	0	--	18.5(77)	1.3(5)	1.5
	48	28.8(60)	0.8(1.6)	3	29.8(61)	0	--	29.0(60)	0	--	29.1(61)	2.1(4.7)	1.25
4	3	2.0(67)	0	--	2.0(67)	0	--	0	0	--	1.0(33)	0	--
	6	3.3(55)	0	--	4.6(77)	0.3(5)	1	4.3(72)	0	--	3.0(50)	0	--
	12	6.0(50)	0	--	5.0(42)	0	--	6.6(54)	0.8(6.3)	3	6.0(50)	0.3(2.1)	1
	24	21.0(86)	1.7(7)	0.6	11.0(46)	0.7(3)	1.0	16.3(68)	1.5(6.3)	5.0	11.5(48)	0.5(2)	1.01
	48	26.0(55)	1.8(38)	4	20.0(42)	0	--	28.3(54)	0.8(1.6)	2.0	26.3(55)	4.5(9.4)	1.57
16	3	2.6(87)	0.3(10)	1	1.7(57)	0	--	1.6(53)	0.3(10)	1	2.0(67)	1.0(33)	0.5
	6	4.6(77)	0.6(10)	2	5.7(95)	0	--	3.6(60)	0.3(5)	1	5.3(88)	3.3(55)	1.0
	12	10.8(90)	3.5(29)	1.33	7.8(65)	0	--	8.0(66)	1.0(83)	1.0	9.0(75)	4.0(33)	4.3
	24	19.4(81)	2.7(11)	1.67	18.0(75)	0.5(2)	1.0	13.3(55)	1.3(5)	1.5	19.1(80)	9.8(41)	1.6
	48	41.0(86)	9.0(19)	2.0	37.0(77)	0.5(1)	2	26.8(56)	1.5(3)	2.0	37.0(77)	17.0(35)	3.9

[a] $\bar{x}$ H.D.: Average number of host deaths.

[b] $\bar{x}$ para.: Average number of F_1 parasitoids emerged.

CHAPTER V
INTERSPECIFIC COMPETITION

The multi-species release program, suggested and evaluated by Doutt and DeBach (1964), contrasts with the single species release program proposed by Turnbull and Chant (1961). Proponents of the multi-species release program contend that the net control effect of using two or more species would be greater than the control attained by releasing only one. There are, however, conflicting arguments regarding the advantages and disagvantages of the release of two or more beneficial species for the control of a single pest species. This chapter contains observations involving the interactions between the four parasitoid species. Based on these observations, recommendations about the species best suited for use as a biological control of A. suspensa are made.

Materials and Methods

The interspecific studies were set up as described in the preceding chapter on superparasitism. Two major groups of experiments were conducted. First, larval hosts were exposed to two or three species simultaneously for 2 hours. Two or three 9 cm diameter sting units with 175±25 larvae in each were presented simultaneously to five males and five females of each of the two or three parasitoid species in 38 x 34 x 20 cm cages. Second, hosts were exposed to different species in a

sequence. Each exposure lasted 2 hours, except in the case of DG which lasted 24 hours. Ten males and ten females of each parasitoid species were put in four cages 38 x 34 x 20 cm. Larvae were then introduced into each of the four cages in the two-species exposure sequences of BL→OC, BL→TD, OC→BL, TD→BL, OC→TD, TD→OC, BL→DG, AND TD→DG. The three species exposure sequences were: BL→OC→TD, BL→TD→OC, OC→BL→TD, OC→TD→BL, TD→BL→OC, and TD→OC→BL. A fourth species was exposed in the same manner as the three-species sequence. After these hosts were removed and had pupated for 48 hours they were then exposed to DG parasitoids. Ten replications were made for each exposure sequence. Samples to be dissected were taken 72-144 hours after their removal from the last species. The remaining samples were reared until adult parasitoids emerged.

Results and Discussion

Experiment I: Simultaneous Exposure Studies

Analyses of dissected and reared samples (Table 33) indicated that when BL and OC (BL/OC) were simultaneously exposed to hosts, BL was dominant. There was no significant difference between dissected and reared samples in terms of percentage of BL parasitism ($X^2=0.14$) and OC parasitism ($X^2=0.7$). Since BL was the dominant species, in terms of aggression and efficiency in searching for hosts, it was considered an extrinsically better competitor than OC. The low multiparasitism percentage made it difficult to determine the intrinsically superior species.

The low percentage of multiparasitism (0.6%) also indicated the species might be able to recognize the presence of each other and avoid

Table 33. Comparison of percent of parasitism between dissected and reared samples when BL and OC were simultaneously exposed.

	Dissected Samples (DS)		Reared Samples (RS)
No. samples	174		2051
No. parasitized (DS)/ No. parasitoids (RS)	67		337
% parasitism	38.5		16.4
No. BL (%)	47(70.2)	NS	247(73.3)
No. OC (%)	21(31.4)	NS	90(26.7)

NS: No significant difference between dissected and reared samples by X^2-test, p=0.05.

multiple parasitization, possibly through external or internal marking substances. However, the true mechanism of interspecific recognition remains unclear, since very little interspecific discrimination has been reported (Price 1970, 1972). In the 47 BL parasitized hosts, 15% were superparasitized. Perfect host discrimination was shown by the OC parasitoids (Table 34).

Analyses of dissected and reared samples indicated that when BL and TD (BL/TD) were simultaneously exposed to hosts, there was no significant difference between the species' success in parasitizing the host (Table 35). This indicated TD and BL were intrinsically comparable species. TD was, however, an extrinsically better competitor than BL since it was able to locate a greater number of hosts (X^2-4.4).

The percentage of multiparasitism (5.4%) (Table 36) in the BL/TD study was greater than that in BL/OC study. This could have been accounted for in several ways: (1) BL may have recognized the presence of OC but not TD; (2) TD may have been unable to recognize the presence of BL; or (3) TD had a tendency to multiparasitize the host in order to avoid some encapsulation, as noted in the multiparasitization of P. bochei (Streams 1971, Streams and Greenberg 1969) and of T. giffardianus (Pemberton and Willard 1918).

The ability of BL parasitoids to discriminate among hosts was demonstrated by the low percent of superparasitism (3%) shown by the insect (Table 36). TD's higher superparasitism percentage (40%) confirmed that in performing host discrimination, it favored parasitized hosts due to their low HCE% (Table 36). No encapsulation of TD parasitoids was found in multiparasitized hosts. This may indicate that TD prefered multiparasitized over superparasitized hosts, since it was

Table 34. The results of dissected samples of BL and OC simultaneous exposure experiment.

Parasitization categories	BL (%)		OC (%)		Total (%)
single species parasitization		46(26.4)		20(11.5)	66(37.9)
1 progeny	39(22.4)		20(11.5)		
>1 progeny	7(4.0)		0		
mulitparasitism		1(0.6)		1(0.6)	1(0.6)
1 progeny	1(0.6)		1(0.6)		
>1 progeny	0		0		
Total		47(27.0)		23(12.1)	67(38.5)
No. superparasitized hosts	7		0		
% superparasitism	14.9%		-		
% multiparasitism	2.1%		4.3%		

No. samples=174

No. parasitized=67

% parasitism=38.5

Table 35. Comparison of percent of parasitism between dissected and reared samples when BL and TD were simultaneously exposed.

	Dissected Samples (DS)		Reared Samples (RS)
No. samples	168		2148
No. parasitized (DS)/ No. parasitoids (RS)	71		329
% parasitism	42.3		15.3
No. BL (%)	32(45.07)	NS	156(47.4)
No. TD (%)	48(67.61)	NS	173(52.6)

NS: No significant difference between dissected and reared samples by X^2-test, p=0.05.

Table 36. The results of dissected samples of BL and TD simultaneous exposure experiment.

Parasitization categories	BL (%)		TD (%)		Total (%)
single species parasitization		23(13.7)		39(23.2)	62(36.9)
1 progeny	22(13.1)		23(13.6)		
>1 progeny	1(0.6)		16(6.6) (HCE(%)=25(64.1))		
multiparasitism		9(5.4)		9(5.4)	9(5.4)
1 progeny	9(5.4)		6(3.6)		
>1 progeny	0(0)		3(1.8) (HCE(%)=0(0))		
Total		32(19.1)		48(28.6)	71(42.3)
No. superparasitized hosts	1		19		
% superparasitism	3%		40%		
% multiparasitism	28.1%		18.8%		

No. samples=168
No. parasitized=71
% parasitism=42.3

easier for TD to avoid encapsulation when it parasitized hosts previously parasitized by other species (Table 36).

When OC and TD (OC/TD) were simultaneously exposed to hosts, a significant difference (X^2=3.86) was found between dissected and reared samples of OC parasitization. Apparently OC was a less effective intrinsic competitor than TD (Table 37). In multi-species parasitization cases most OC progeny were found to be scarred by prior attacks. The multiparasitism percentage (8.2%) (Table 38) was similar to that of BL/TD (5.4%) (Table 36) (t=0.97). This indicated that either OC and TD could not recognize the presence of each other, or TD had a tendency to multiparasitize the host. TD was an extrinsically better competitor than OC since it was able to locate a greater number of hosts (47 vs. 35, X^2=4.11) (Table 37).

Both OC and TD superparasitized hosts (Table 38). TD showed a smaller tendency to superparasitize when it was simulatneously exposed with OC (23.4%) (Table 38) than when it was exposed with BL (40%) (Table 36). BL demonstrated a smaller degree of superparasitism (3%) when it was exposed with TD than that when it was exposed with OC (15%) (Table 34). The reasons remain unknown.

The results of the exposure of hosts to three species simultaneously are given in Tables 39 and 40. The likelihood that three species would multiparasitize the same host was relatively small (0.3%) compared to two-species multiparasitism cases (10.1%). The majority of parasitism was due to a single species (Table 40).

BL was a better intrinsic competitor than OC and TD, since no significant difference in BL parasitism was found in the dissected and reared samples (X^2=0.12). However, the reared samples of OC and TD showed

Table 37. Comparison of percent of parasitism between dissected and reared samples, when OC and TD were simultaneously exposed.

	Dissected Samples (DS)		Reared Samples (RS)
No. samples	145		1552
No. parasitized (DS)/ No. parasitoids (RS)	70		183
% parasitism	48.3		11.8
No. OC (%)	35(50.0)	*	16(36.1)
No. TD (%)	47(67.1)	NS	117(63.9)

*: Significant difference between dissected and reared samples by X^2-test, p=0.05.
NS: No significant difference between dissected and reared samples by X^2-test, p=0.05.

Table 38. The results of dissected samples of OC and TD simultaneous exposure experiment.

Parasitization categories	OC (%)		TD (%)		Total (%)
Single species parasitization		23(15.9)		35(24.1)	58(40)
1 progeny	21(14.5)		26(17.9)		
>1 progeny	2(1.4)		9(6.2) (HCE(%)=17(48.6)		
multiparasitism		12(8.2)		12(8.2)	12(8.2)
1 progeny	10(6.8)		10(6.8)		
>1 progeny	2(1.4)		2(1.4) (HCE(%)=0(0))		
Total		35(24.1)		47(32.3)	70(48.3)
No. superparasitized hosts	4		11		
% superparasitism	11.4%		23.4%		
% multiparasitism	34.3%		25.6%		

No. samples=145

No. parasitized=70

% parasitism=48.3

Table 39. Comparison of percent of parasitism between dissected and reared samples when BL, OC and TD were simultaneously exposed.

	Dissected Samples (DS)		Reared Samples (RS)
No. samples	365		2809
No. parasitized (DS)/ No. parasitoids (RS)	187		407
% parasitism	51.2		14.5
No. BL (%)	131(70.1)	NS	297(73.0)
No. OC (%)	38(20.3)	*	34(8.4)
No. TD (%)	57(30.5)	*	76(18.7)

NS: No significant difference between dissected and reared samples by X^2-test, p=0.05.

*: Indicates the significant difference between dissected and reared samples in percent of parasitism by X^2-test, p=0.05.

Table 40. The results of dissected samples of BL, OC and TD simultaneous exposure experiment.

Parasitization categories	BL (%)	OC (%)	TD (%)	Total (%)
single species parasitization	96(26.3)	27(7.4)	26(7.1)	149(40.8)
1 progeny	80(22)	25(6.8)	18(4.9)	
>1 progeny	16(4.3)	2(0.6)	8(2.2) (HCE(%)=14(54))	
multiparasitism				
3 spp.	1(0.3)	1(0.3)	1(0.3)	1(0.3)
2 spp.	34(9.3)	10(2.7)	30(8.2)	37(10.1)
1 progeny	20(5.5)	10(2.7)	27(7.4)	
>1 progeny	15(4.1)	1(0.3)	4(1.2)	
Total	131(35.9)	38(10.4)	57(15.6)	187(51.2)
No. superparasitized hosts	31	3	12	
% superparasitism	23.7%	7.9%	21.1%	
% multiparasitism	26.7%	29.0%	54.4%	

No. samples=365

No. parasitized=187

% parasitism=51.2

significantly less parasitism since $X^2=6.98$ and $X^2=4.57$, respectively. In searching for hosts, BL demonstrated that it was a better extrinsic competitor than the other two species. Unlike BL which found 36% of the hosts (131/365), TD found only 16% (57/365) and OC found only 10% (38/365) of the hosts. Interference competition restricted the searching efficiencies of TD and OC when three species were involved since both had found fewer hosts then than when only two species were involved.

Superparasitism was encountered in these three species to a smaller extent than multiparasitism. Whether these three species had a tendency to multiparasitize the hosts was studied in the sequential exposure experiments. Multiparasitism was apparently beneficial to the survival of TD in that it facilitated avoidance of encapsulation.

The differences between the percent of parasitized hosts found in dissected samples and percent of parasitoid which emerged from reared samples may be due to factors that were discussed in Chapter II (Table 10).

The total mortality observed in the two-species simultaneous exposure experiments is given in Table 41. Total mortality was lower when BL was released with another species than when BL was released alone. Similar results were found when OC was released alone and with another species. In contrast, TD was a more effective control agent when it was released with another species than when it was released alone. These results indicated that when dealing with BL and OC, a simultaneous multispecies release might be detrimental to the control efficacy of a single species release. The total mortality of the hosts was 74.5% when three species were released simultaneously. This mortality rate was higher than when only two of the three species were released at the same

Table 41. Total mortality due to single species or any of two species exposed simultaneously.

	BL	OC	TD
BL	74.5		
OC	59.3	65.4	
TD	53.4	57.9	42.2

time. Further, it was equal to the host mortality obtained when BL was released alone (74%). Again, these results demonstrated the necessity to properly select biocontrol agents used in releases designed to extablish natural enemy species.

Experiment II: Sequential Exposure Studies

In nature, simultaneous multi-species oviposition is rare. Therefore, in order to minimize the effect of mutual interference and to obtain detailed information on interspecific host discrimination ability, experiments involving the sequential exposure of hosts to different species were carried out. The percentages of parasitism found in dissected and reared samples are summarized in Table 42.

Study of BL→OC, and OC→BL

When hosts were exposed to OC after being removed from the BL cage (BL→OC), the percentage of OC superparasitism (8.1%) was smaller than that of multiparasitism (10.7%). Since 27.7% of the hosts remained unparasitized, apparently OC did not search all the hosts before it multiparasitized hosts already attacked by BL (Table 30). OC multiparasitized the hosts regardless ot the number of BL progeny present in the hosts--5.8% of the hosts had previously been superparasitized by BL and 4.7% had been singly parasitized by BL. This information indicated OC probably could not detect the number present in the host and was unable to discriminate interspecifically. A majority of hosts parasitized by OC were not previously attacked by BL (167/196=85%), therefore, OC did exercise an ability to distinguish parasitized hosts from healthy ones (Table 43).

Table 42. Comparison of percent of parasitism between dissected and reared samples when hosts were presented to parasitoids in sequence.

Experiments	Dissected samples						Reared samples						Total Mortality (%)
	No. samples	No. parasitized hosts(%)	% parasitism				No. samples	No. parasitoid emerged(%)	% parasitism				
			BL	OC	TD	DG			BL	OC	TD	DG	
BL ck	598	430	71.95				4717	1871	39.49				74.45
OC ck	633	324		51.12			4951	322		6.47			65.43
TD ck	583	433			73.86		5142	851			16.53		42.16
DG ck	379	133				33.12	4291	838				19.92	42.70
BL→OC	271	196(72)	70.41	44.39			1979	591(30)	91.88*	8.12*			76.10
BL→TD	269	215(80)	88.37		34.88		1800	329(18)	93.01		6.99*		74.80
BL→DG	254	199(78)	91.96			34.67	1563	529(34)	72.97*			27.03	80.80
OC→BL	270	186(69)	43.55	70.43			1594	267(17)	78.65*	21.35*			76.70
OC→TD	243	153(63)		82.35	41.83		1385	84(6)		47.62*	52.38		66.14
OC→DG	232	176(76)		69.94		41.62	1554	312(20)		21.15*		78.85*	74.30
TD→OC	262	178(68)		70.22	77.53		1807	155(9)		22.58*	77.42		56.90
TD→BL	272	210(77)	68.57		56.19		1745	460(26)	75.65		24.35*		73.60
TD→DG	267	180(67)			75.56	46.67	1819	458(25)			22.91*	77.07*	50.70

Table 42--Extended.

BL→OC→TO	347	299(86)	77.36	32.09	12.50		1751	547(31)	90.41	7.11*	2.48*		85.80
BL→TD→OC	350	293(84)	80.42	37.37	32.87		2074	582(28)	92.20	5.44*	2.36*		79.60
OC→BL→TD	364	272(75)	52.21	50.00	27.94		1901	347(18)	74.64*	15.85*	9.51*		74.10
OC→TD→BL	338	250(74)	43.60	54.00	41.20		1759	239(14)	71.55*	15.90*	12.55*		78.30
TD→OC→BL	372	303(82)	35.64	54.79	63.37		1901	251(13)	60.12*	14.34*	25.50*		75.40
TO→BL→OC	363	276(76)	57.97	35.14	58.70		1742	265(15)	75.47*	6.04*	18.49*		73.70
BL→OC→TD→DG	274	238(87)	65.55	38.24	17.65	27.73	1463	423(29)	61.94	5.91*	3.07*	29.08	88.00
BL→TD→OC→DG	262	235(90)	73.62	40.00	37.87	25.11	1395	323(23)	58.20	5.57*	7.12*	29.10	89.40
OC→BL→TO→DG	274	224(82)	54.45	52.23	25.89	22.32	1321	240(18)	56.67	10.83*	4.17*	28.33	84.40
OC→TD→BL→DG	271	223(82)	36.77	37.40	34.08	26.91	1347	280(21)	24.64*	11.43*	11.79*	52.14*	83.70
TD→OC→BL→DG	262	219(84)	19.27	54.34	40.64	31.05	1364	231(17)	29.78	11.65*	15.15*	41.29*	83.90
TO→BL→OC→DG	273	235(86)	52.34	36.60	47.23	33.62	1581	389(25)	26.22*	6.43*	14.65*	52.70*	87.80

*Indicates the significant difference between reared and dissected samples in the same experiment of the same species by X^2-test, $p=0.05$.

The OC→BL situation showed a similar result in that BL superparasitized (10.4%) (5.6+4.8=10.4%) or multiparasitized (9.6%) the hosts before it searched all the hosts (Table 43). Approximately 31% of the hosts remained unparasitized as a result. The similar degrees of superparasitism and multiparasitism, and the high single-species parasitism (86%) indicated that BL probably lacked an interspecific discrimination ability but was able to distinguish between healthy and parasitized hosts. BL also lacked the ability to detect the number of progeny or eggs which existed in the hosts, since in 50% of the hosts (13 out of 26) were parasitized with one OC and 50% were parasitized with more than one OC.

These results conflict with the assumption that OC and/or BL performed interspecific discrimination in the BL/OC and BL/OC/TD simultaneous exposure experiment where the multiparasitism of BL/OC was low. This was probably caused by interspecific interference which restricted the searching behavior of both species when the species were simultaneously presented to the hosts.

In the BL→OC and OC→BL cases, neither species appeared to be a superior extrinsic competitor in terms of searching hosts. About 51% of the hosts were found by BL when it was the species exposed first, and about 30% of the hosts were found by BL when it was the species exposed second. OC found about 49% of the hosts when it was the species exposed first and 32% when it was the second (Table 30). A sequence effect might have influenced this behavior since the first exposed species had an advantage in ovipositing in more hosts.

When the percentage of parasitism revealed by dissected and reared samples of BL→OC and OC→BL were compared, the percentage of BL was

Table 43. The results of dissected samples of experiments BL→OC and OC→BL.

Exposure sequence	Parasitization categories	BL (%)		OC (%)		Total (%)
BL→OC	single species parasitization		109(40.2)		58(21.4)	167(61.6)
No. samples=271	1 progeny	80(29.5)		44(16.2)		
	>1 progeny	29(10.7)		14(5.2)		
No. parasitized=196	multiparasitism		29(10.7)		29(10.7)	29(10.7)
% parasitism=72.3	1 progeny	16(5.4)		21(7.8)		
	>1 progeny	13(4.7)		8(2.9)		
	Total		138(50.9)		87(32.1)	196(72.3)
OC→BL	single species parasitization		55(20.4)		105(38.9)	160(59.3)
No. samples=270	1 progeny	40(14.8)		87(32.2)		
	>1 progeny	15(5.6)		18(6.7)		
No. parasitized=186	multiparasitism		26(9.6)		26(9.6)	26(9.6)
% parasitism=68.9	1 progeny	13(4.8)		18(6.7)		
	>1 progeny	13(4.8)		8(2.9)		
	Total		81(30.0)		131(48.5)	186(68.9)

significantly greater in the reared samples in both situations while the percentage of OC was significantly smaller. This indicated that, overall, BL was the superior species in intrinsic competition, regardless of the order in which it was exposed to the host. The sequence effect was therefore less important than the species effect.

Study of BL→TD and TD→BL

The results of the experiments on the effect of the order of exposure on the behavior of BL and TD was given in Table 44. In BL→TD cases, the superparasitism percentage of TD (6.3%) was significantly smaller than multiparasitism (18.6%) (X^2=6.08), although the TD female repeatedly oviposited on multiparasitized hosts (11.2%). The higher multiparasitism percentage meant that TD had an interspecific discrimination ability. The avoidance of encapsulation, indicated by zero or low HCE% in BL/TD cases, was the major advantage of TD multiparasitism. In the 32 BL/TD interaction cases revealed during dissection, TD killed BL in 24 cases. The dead BL had scars on their bodies. In only four cases were TD killed by BL. In the remaining four cases, both BL and TD were found dead with scars. This indicated that if TD survived encapsulation they had a better chance to defeat BL. TD showed a preference to multiparasitize BL-parasitized hosts. Many of the TD progeny were wasted in superparasitism, thus TD visited a smaller number of hosts than BL even though TD was likely to defeat BL in the BL/TD situations. Therefore, compared to BL, TD was a superior intrinsic competitor but an inferior extrinsic competitor.

TD showed some preference to oviposite in BL singly-parasitized hosts over BL superparasitized ones (12.6% vs. 5.9%, X^2=3.1, p=0.1). Thus, TD had a greater chance of winning when competing with only one BL. This

Table 44. The results of dissected samples of experiments BL→TD and TD→BL.

Exposure sequence	Parasitization categories	BL (%)		TD (%)		Total (%)
BL→TD	single species parasitization		140(52.0)		25(9.3)	165(61.3)
No. samples=269	1 progeny	87(32.3)		8(3.0)		
	>1 progeny	53(19.7)		17(6.3)		
No. parasitized=215				(HCE(%)=15(60))		
	multiparasitism		50(18.6)		50(18.6)	50(18.6)
% parasitism=79.9						
	1 progeny	34(12.6)		21(7.4)		
	>1 progeny	16(5.9)		29(11.2)		
				(HCE(%)=0(0))		
	Total		190(70.6)		75(27.9)	215(79.9)
TD→BL	single species parasitization		92(33.8)		66(24.3)	158(58.1)
No. samples=272	1 progeny	56(20.6)		31(11.4)		
	>1 progeny	36(13.2)		35(12.9)		
No. parasitized=210				(HCE(%)=47(71))		
	multiparasitism		52(19.1)		52(19.1)	52(19.1)
% parasitism=77.2						
	1 progeny	33(12.1)		26(9.6)		
	>1 progeny	19(7.0)		26(9.5)		
				(HCE(%)=9(17.3))		
	Total		144(52.9)		118(43.4)	210(77.2)

was evident when 22 out of 24 BL were killed in BL/TD interactions. This indicated TD probably was able to "detect" the number of BL larvae or eggs in the host and oviposited those with a low number of eggs.

Comparisons between the percentage of parasitism revealed by dissected and reared samples (Table 42) indicated that, although no significant difference was found in BL parasitism, a significant difference was found in TD. The analysis also showed that fewer hosts were found by TD than BL, indicating BL was the superior species of the two. TD had an additional advantage in physical combat since it possessed a longer first instar stage. This extended the period in which it was competitive.

When BL was introduced as the second species (TD→BL), BL performed significantly better in selecting healthy hosts over parasitized hosts (33.8% vs. 19.1%, $X^2=4.08$, $p=0.05$). It showed no preference for TD-superparasitized or TD-singly parasitized hosts (9.5% vs. 9.5%). By distinguishing parasitized and non-parasitized hosts, BL exercised host discrimination ability. No evidence was found, however, to show BL performed interspecific discrimination or had an ability to detect the number of progeny in the hosts.

When reared samples were analyzed (Table 42), there was no significant difference in BL. The significant decrease found in the TD reared samples therefore meant BL was intrinsically superior to TD. In the TD BL study, TD did not take full advantage of multiparasitism in all BL/TD cases for in some hosts all TD progeny were killed by encapsulation. Thus no TD adult could have been expected to emerge (HCE%=17.3%) (Table 31). This finding showed the failure of TD to take full advantage of multiparasitism might have been due to the asynchronism

of encapsulation and the release of the antihost defense material by BL, although the behaviors occurred only 2 to 4 hours apart. The reason for this asynchronism is unknown and further study in this area could be valuable.

It has frequently been found that the first species to be released had an advantage over later species since it could attack more hosts. The present study supported this conclusion (Table 44). The effect of order might be important in TD-associated multiparasitism. When TD was the second species to be exposed to the host, it could select the host type and reduce its chances of encapsulation. But this selection advantage was not corroborated by the findings in the reared samples. This could have been because TD expended too much energy and wasted time searching for BL-parasitized hosts with low numbers of progeny instead of using more available hosts. Another explanation could have been that TD's competitive ability was different from that observed in the BL TD study. In 33 BL/TD interaction cases, TD were killed by BL in 14 cases (42.4%), and BL were killed by TD in 16 cases (48.5%). In the other three cases both species were killed and showed scars. Thus in the TD BL cases, BL and TD were equally competitive.

Study of TD→OC and OC→TD

In TD→OC cases, the multiparasitism percentage of OC was significantly higher than single-species parasitism by OC (32.4% vs. 15.3%, $X^2=6.13$, $p=0.05$) (Table 45). Since multiparaistism did not appear to be of any advantage to OC, the high multiparasitism percentage might have been due to some other causes. One explanation could be lack of interspecific discrimination ability. This, however, could not have been the only reason, otherwise the multiparasitism percentage should have

Table 45. The results of dissected samples of experiments TD→OC and OC→TD.

Exposure sequence	Parasitization categories	TD (%)		OC (%)		Total (%)
TD→OC	single species parasitization		53(20.2)		40(15.3)	93(35.3)
No. samples=262	1 progeny	20(7.6)		26(9.9)		
	>1 progeny	33(12.6)		14(5.3)		
No. parasitized=178		(HCE(%)=39(73.6))				
	multiparasitism		85(32.4)		85(32.4)	85(32.4)
% parasitism=67.9						
	1 progeny	49(18.7)		63(24.0)		
	>1 progeny	36(13.8)		22(8.4)		
		(HCE(%)=2(2.4))				
	Total		138(52.6)		125(47.7)	178(67.9)
OC→TD	single species parasitization		27(11.1)		89(36.5)	116(47.6)
No. samples=243	1 progeny	7(2.9)		62(25.4)		
	>1 progeny	20(8.2)		27(11.1)		
No. parasitized=153		(HCE(%)=18(66.7))				
	multiparasitism		37(15.2)		37(15.2)	37(15.2)
% parasitism=62.7						
	1 progeny	16(6.6)		31(12.7)		
	>1 progeny	21(8.6)		6(2.5)		
	Total		64(26.3)		126(51.7)	153(62.8)

been close to the single-species parasitism percentage. It is also possible that TD left insufficient marking material to allow detection by OC. The high multiparasitism percentage could also have been caused by TD's tendency to lay its eggs in the postcephalic third or fourth segmental area (CI) and any internal marking material was only slowly distributed. OC randomly selected the oviposition site. Since the likelihood of it selecting the CI area was only 15% (24/156, Table 4), OC would then fail to detect the presence of TD in most ovipositions. The latter two factors might explain the fact that OC laid only one egg in most multiparasitization hosts (Table 45). It could not recognize the presence of TD, and accepted the TD-parasitized hosts.

In terms of searching efficiency, OC and TD performed with similar ability. TD attacked 52.6% of the hosts and OC attacked 47.7% of the hosts (Table 45). But when comparing the information on the percentage of parasitism provided by dissected and reared samples, a significant decrease was found in reared samples of OC but not of TD (Table 42). This indicated that TD was a better intrinsic competitor than OC. The success of TD survival was mainly attributed to OC's inability to discriminate among hosts.

In OC→TD cases, the multiparasitism percentage was not significantly higher than the superparasitism percentage of TD (15.2% vs. 8.2%, $X^2=2.5$, $p=0.05$), although TD demonstrated a tendency to select OC parasitized hosts. TD demonstrated a strong tendency to select hosts singly parasitized by OC (31/37=84%) (Table 45). In 12 TD/OC interaction cases, TD won eight times. Therefore, since TD preferred hosts occupied by only one OC, it would encounter limited competition and its likelihood of defeating the OC would be improved. This result confirmed the information

observed in the reared samples (Table 42). In those, OC showed a significant decrease of parasitism when compared to dissected samples.

The failure of TD to win in four cases was due to encapsulation. In those instances the host defense material released by some OC was apparently not sufficient to protect TD from encapsulation. The preference for single-OC-parasitized hosts was an indication that TD had the ability to detect the number of progeny.

In either TD→OC or OC→TD cases, overall, TD was the superior species. This was demonstrated by the fact that a higher percentage of TD parasitoids emerged. OC, however, was extrinsically superior in searching for hosts in OC→TD cases (Table 45).

From these two-species, sequential exposure studies of the larval parasitoids, it might be said that BL>TD>OC compare in terms of competitive ability along a larval guild.

Study of BL→DG, OC→DG, and TD→DG

Results of the release of DG after the other larval species are given in Table 46. The percentage of superparasitism by DG was 1.7% in the OC→DG cases, and zero in BL→DG and TD→DG cases. In all the multi-species parasitization cases, DG sometimes laid more than one egg, However, in all of those >1 DG progeny cases, no more than two DG eggs were ever found. The percentage of DG progeny groups with more than one egg was relatively low (4.4% in BL/DG, 3.0% in OC/DG, 1.1% in TD/DG). In the vast majority of cases, DG only laid one egg per host regardless of whether the host had been parasitized by another species. These findings indicate DG exercised nearly perfect intraspecific host discrimination in avoiding superparasitism but not interspecific discrimination. The absence of this latter ability could have been due to the fact that the

Table 46. The results of dissected samples of experiments BL→DG, OC→DG, and TD→DG.

Exposure sequence	Parasitization categories	Larval species		DG (%)	Total (%)
		BL(%)			
BL→DG	single species parasitization	130(51.2)		16((6.3)	146(57.5)
No. samples=254	1 progeny	94(37)		16(6.3)	
	>1 progeny	36(14.2)		0(0.0)	
No. parasitized=199	multiparasitism	53(20.9)		53(20.9)	53(20.9)
% parasitism=78.3	1 progeny	37(14.6)		42(16.5)	
	>1 progeny	16(6.3)		11(4.4)	
	Total	183(72.1)		69(27.2)	199(78.4)
		OC(%)			
OC→DG	single species parasitization	101(43.5)		52(22.4)	153(65.9)
No. samples=232	1 progeny	74(31.9)		48(20.68)	
	>1 progeny	27(11.6)		4(1.7)	
No. parasitized=176	multiparasitism	23(9.91)		23(9.9)	23(9.9)
% parasitism=75.9	1 progeny	13(5.6)		16(6.9)	
	>1 progeny	10(4.3)		7(3.0)	
	Total	124(53.41)		75(32.3)	176(75.8)

Table 46--Extended.

TD→DG		TD(%)				
	single species parasitization		96(36)		44(16.4)	140(52.4)
No. samples=267	1 progeny	30(11.2)		44(16.4)		
	>1 progeny (HCE=85(88.5%))	66(24.7)		0(0.0)		
No. parasitized=180	multiparasitism		40(15)		49(15)	
% parasitism=67.4						
	1 progeny	18(6.7)		37(13.9)		
	>1 progeny (HCE=38(95%))	22(8.2)		3(1.1)		
	Total		136(51)		84(31.4)	180(67.4)

marking material deposited by larval parasitoids had faded away during pupation or was contained internally and DG could not detect it with its shorter ovipositor (0.25 cm, Table 2).

In some interspecific interactions between BL and DG (n=45), or between OC and DG (n=20) observed through dissection, DG was a better intrinsic competitor than BL and OC. DG fed externally on the pupa inside the puparium and experienced no direct contact with BL or OC. When DG started feeding it either caused a nutritional inadequacy, or changed the biochemical composition of the host's body which then resulted in the retardation of normal development of BL or OC. DG-damaged, true pupa started turning dark brown within 48 to 72 hours after the first DG instar hatched, while BL, OC, or TD parasitized hosts did not turn dark.

In TD→DG experiments, 38 cases were observed through dissection. DG again was a better intrinsic competitor than TD. The death of TD was not associated with DG feeding habits but due to encapsulation. TD oviposited first, at least 48 hours before DG. Nearly all the newly hatched first instar larvae were found encapsulated and the HCE% was as high as 88.5% in single-species and 95% in multi-species parasitism (Table 46). Usually the encapsulation process would not start until 48 to 60 hours after oviposition when the first instar of TD hatched. Therefore, in this study, most encapsulation might have occurred after DG oviposition. This meant that either DG did not produce any antihost defense material or did produce some but in an insufficient amount and/or it was distributed slowly from the caudate end to the front area where the first instar of TD was hatched.

In comparing information on the percentage of parasitism obtained from dissected and reared samples of DG associated cases, DG showed either no difference (BL→DG) or a significant increase (OC→DG, TD→DG) in reared samples while all the other species showed a significant decrease (Table 42).

Given the information obtained from all the two-species sequential exposure experiments, DG ranked the highest in competitive ability, followed by BL, TD, and then OC.

Study of BL→OC→TD and BL→TD→OC

In the BL→OC→TD experiments, OC was the species exposed to the host second. Its multiparasitism percentage (10.1+0.9=11%) was higher than superparasitism percentage (5.5%), and it evenly distributed its progeny in BL-parasitized (11%) and non-BL-parasitized (13.3%) hosts (Table 47). These results were similar to the findings from the BL→OC experiments (Table 43) which showed that OC exercised a host discrimination ability in differentiating the parasitized from healthy hosts but possessed no interspecific discrimination ability. The host discrimination ability of OC was somewhat weak, since only 7.8% of the hosts were attacked by a single OC progeny. This might have been due to the random behavior pattern exhibited by OC when OC accidentally landed on a surface with more BL-parasitized hosts than healthy hosts. OC would start her localizing movement on that area, resulting in more multiparasitization than single-species parasitization. In 15 BL-parasitized hosts, ring-structure damage was found, and the hatched BL progeny were dead but without evidence of scars. Usually when the ring-structure damage due to BL was present, no BL could be expected to be found. Therefore, OC was the principle species causing ring-structure damage.

Table 47. The results of dissected samples of experiments BL→OC→TD and BL→TD→OC.

Exposure sequence	Parasitization categories	BL (%)	OC (%)	TD (%)	Total (%)
	single species parasitization	178(51.3)	46(13.3)	10(2.9)	234(67.5)
	1 progeny	112(32.3)	27(7.8)	5(1.4)	
BL→OC→TD	>1 progeny	66(19.0)	19(5.5)	5(1.4) (HCE(%)=5(50))	
No. samples=347	multiparasitism				
No. parasitized=299	3 spp.	3(0.9)	3(0.9)	3(0.9) (HCE(%)=0(0))	3(0.9)
% parasitism=86.2	2 spp.	51(14.7)	46(13.3)	27(7.8)	62(17.8)
	BL/OC*	35(10.1)	35(10.1)		
	BL/TD	16(4.6)		16(4.6)	
	OC/TD		11(3.2)	11(3.2) (HCE(%)=2(6.7))	
	Total	232(66.9)	95(27.5)	40(11.6)	299(86.2)
	single species parasitization	138(39.4)	25(7.1)	14(4.0)	177(50.5)
	1 progeny	83(23.7)	19(5.4)	3(0.9)	
BL→TD→OC	>1 progeny	55(15.7)	6(1.7)	11(3.1) (HCE(%)=12(8.6))	
No. samples=350	multiparasitism				

Table 47--Extended.

No. parasitized=293	3 spp.		33(9.4)	33(9.4)	33(9.4) (HCE(%)=2(6))	33(9.4)
% parasitism=83.7	2 spp.		62(17.7)	50(14.3)	54(15.4)	83(23.7)
	BL/OC	29(8.3)	29(8.3)			
	BL/TD	33(9.4)		33(9.4)		
	OC/TD		21(6.0)	21(6.0) (HCE(%)=0(0))		
	Total		243(66.5)	108(30.8)	101(28.8)	293(83.6)

* BL/OC = BL and OC multiparasitized the same host.
BL/TD = BL and TD multiparasitized the same host.
OC/TD and OC and TD multiparasitized the same host.

TD exhibited host discrimination and favored multiparasitization (0.9+7.8=8.7%) over superparasitization or healthy hosts (2.9%) (Table 47). No preference was shown by TD in selecting BL- or OC-parasitized hosts (4.6% vs. 3.2%, X^2=0.13). As single-species parasitized hosts 50% of TD would not be expected to produce adults due to the fact that HCE% was as high as 50%. In the three-species parasitism the HCE% was zero and in the two-species parasitism the HCE% was 6.7%.

In 35 multi-species competition cases observed through dissection (Table 48), BL and TD were about equally likely to defeat one another in multiparasitized hosts. OC was less competitive compared to the other two. Therefore, in intrinsic competitive ability, the guild would be BL=TD>OC. TD, however, was disadvantaged by the possibility of encapasulation and the waste of eggs and hosts caused by superparasitism. BL was the overall superior competitor among the three species. When dissected and reared samples were compared, there were significant decreases of TD and OC in terms of parasitism percentage in reared samples, but no difference was found in BL. Also, BL was the species which most often dominated in both samples. Thus BL was an intrinsically and extrinsically better competitor than the other two species. The least successful species with regard to parasitism was TD. It had a smaller degree of decreases in reared samples than OC (X^2=8.03 vs. X^2=19.4) (Table 42). The reason for the small percentage of TD parasitism might be related to the sequence effect in so far as TD took a longer time to perform interspecific discrimination. Data obtained by observing interactions which involved TD indicated that after BL, TD should be considered the next best species. The larval guild according to competitive ability was BL>TD>OC.

Table 48. The outcome of observed interactions when exposure sequence was BL→OC→TD.

Species combination	BL +	BL -*	OC +	OC -	TD +	TD -	Total
BL/OC/TD	3	0	0	3	3	0	3
BL/OC	15	4	3	16			19
BL/TD	3	6			5	4	9
OC/TD			0	4	4	0	4
Total	21	10	3	20	12	4	35
(+)%	68%		13%		75%		

*+ = "alive"; - = "killed."

Table 49. The outcome of observed interactions when exposure sequence was BL→TD→OC.

Species combination	BL +	BL -*	OC +	OC -	TD +	TD -	Total
BL/OC/TD	13	2	0	15	15	0	15
BL/OC	13	6	6	13			19
BL/TD	12	16			16	12	28
OC/TD			4	7	7	4	11
Total	38	24	10	35	38	16	73
(+)%	61%		22%		70%		

*+ = "alive"; - = "killed."

In BL→TD→OC cases (Table 47), TD still showed a stronger tendency toward multiple parasitism than superparasitism or single parasitization (24.8% vs. 4.0%, X^2=9.6). This reconfirmed all the previous TD-associated findings. One could conclude that TD exhibited cleptoparasitic behavior. This cleptoparasitic behavior served TD as a survival strategy. Only about 6% of the three-species parasitized hosts and in none of the two-species parasitized hosts were all progeny of TD completely encapsulated. In contrast, the HCE% was 86% when the host was parasitized by TD alone.

When OC was the species exposed to the host last, its host discrimination ability again seemed somewhat weakened since OC attacked previously parasitized hosts more readily (23.7+1.7=25.4%) than when it was the species exposed second (11+5.5=16.5%). This response was probably due to the fact that fewer healthy hosts were available and/or OC's localizing behavior.

In the observed multispecies interactions (Table 49), TD was comparable to BL. OC was weakest of the three. When dissected and reared samples were compared (Table 42), BL remained the highest parasitism percentage species in both samples. TD and OC were only a few percentage points apart but were well behind BL, and there were significant decreases of these two species in reared samples. Therefore, the larval guild for this study should have been BL>TD=OC.

Study of OC→BL→TD and OC→TD→BL

Disregarding OC as the first introduced species, the results of the experiments on the reverse release order of TD and BL were similar to the findings of BL→TD and TD→BL (Table 44).

When BL was the second introduced species, it performed host discrimination by choosing OC-unattacked hosts (23.9+5.8=29.7%) rather than to multiparasitized the host (1.9+7.4=9.3%) or to superparasitize hosts (10.2%) (Table 50). The similar multiparasitism and superparasitism percentages confirmed that BL only exercised intraspecific discrimination.

TD exercised more interspecific discrimination than intraspecific discrimination (13.2% vs. 4.4%, $X^2=4.4$) but it showed no preference for BL-parasitized as opposed to OC-parasitized hosts when TD was introduced as the third species.

In 45 observed multi-species interactions (Table 51), the results were similar to the previous conclusion that TD was comparable to BL, and OC was the most inferior of the three.

OC was extrinsically comparable with BL in terms of searching for hosts when OC was the first exposed species. OC found 37.3% of the hosts and BL found 39% of the hosts. OC, however, was defeated by BL and TD in most observed cases. TD ranked last in both dissected and reared samples (Table 42), but compared to OC, TD experiences a smaller decrease in reared samples ($X^2=12.2$ vs. $X^2=23.3$). TD also had a better chance of winning in observed interaction cases. TD's competitive ability fell between the abilities of BL and OC. Thus, in this study, the larval guild should have been BL>TD>OC.

In the OC→TD→BL cases, as a cleptoparasitoid, TD preferred multiparasitism over superparasitism. The percentage of multiparasitism was therefore 12.2% (4.4+7.7), compared to a superparasitism percentage of 3.6. The HCE% was also less in multiparasitization cases (Table 50).

Table 50. The results of dissected samples of experiments OC→BL→TD and OC→TD→BL.

Exposure sequence	Parasitization categories	BL (%)	OC (%)	TD (%)	Total (%)
	single species parasitization	87(23.9)	82(22.5)	28(7.7)	197(54.1)
	1 progeny	50(13.7)	62(17.0)	12(3.3)	
OC→BL→TD	>1 progeny	37(10.2)	20(5.5)	16(4.4) (HCE(%)=22(79%))	
No. samples=364	multiparasitism				
No. parasitized=272	3 spp.	7(1.9)	7(1.9)	7(1.9)	7(1.9)
% parasitism=74.7	2 spp.	48(13.2)	47(12.9)	41(11.3)	68(18.7)
	BL/OC*	27(7.4)	27(7.4)		
	BL/TD	21(5.8)		21(5.8)	
	OC/TD		20(5.5)	20(5.5) (HCE(%)=2(4%))	
	Total	142(39.0)	136(37.3)	76(20.9)	272(74.7)
	single species parasitization	53(15.7)	80(23.7)	35(10.4)	168(49.8)
	1 progeny	39(11.5)	63(18.6)	23(6.8)	
OC→TD→BL	>1 progeny	14(4.1)	17(5.0)	12(3.6)	
No. samples=338	multiparasitism				

Table 50--Extended.

No. parasitized=250	3 spp.		15(4.4)	15(4.4)	15(4.4) (HCE(%)=2(13))	15(4.4)
% parasitism=74.0	2 spp.		41(12.1)	40(11.8)	53(15.7)	67(19.8)
	BL/OC	14(4.1)	14(4.1)			
	BL/TD	27(8.0)		27(8.0)		
	OC/TD		26(7.7)	26(7.7) (HCE(%)=1(1.5%))		
	Total		109(32.2)	135(39.9)	103(30.5)	250(74.0)

* BL/OC = BL and OC multiparasitized the same host.
BL/TD = BL and TD multiparasitized the same host.
OC/TD = OC and TD multiparasitized the same host.

Table 51. The outcome of observed interactions when exposure sequence was OC → BL → TD.

Species combination	BL		OC		TD		Total
	+	-*	+	-	+	-	
BL/OC/TD	4	2	2	4	6	0	6
BL/OC	16	3	3	16			19
BL/TD	3	4			4	3	7
OC/TD			1	12	12	1	13
Total	23	9	6	42	22	4	45
(+)%	78%		16%		85%		

*+ = "alive"; - = "killed."

Table 52. The outcome of observed interactions when exposure sequence was OC → TD → BL.

Species combination	BL		OC		TD		Total
	+	-*	+	-	+	-	
BL/OC/TD	9	6	8	7	13	2	15
BL/OC	8	1	1	8			9
BL/TD			1	13	13	1	14
OC/TD	1	6			6	1	7
Total	18	13	10	28	32	4	45
(+)%	58%		26%		89%		

*+ = "alive"; - = "killed."

When BL was the species introduced last, the multiparasitism percentage (4.4+15.7=20.1%) was greater than when BL was the species introduced second (9.3%, Table 50). Also, when introduced last, BL found fewer hosts than when it was exposed first (Table 47) or second (Table 50). These data show that BL exercised intraspecific discrimniation but not interspecific discrimination.

In this study, TD was usually able to defeat the other species when species interactions occurred (Table 52). This ability compensated for the fact that it had the smallest percentage of parasitism in both dissected and reared samples (Table 42).

When dissected and reared samples were compared, BL showed a significant increase in the reared samples (X^2=17.92), while the other two species showed significant decreases (Table 42). Of those two species, the decrease in TD was smaller (X^2=8.4 vs. X^2=26.9).

The OC→TD→BL results indicated the parasitoids should be ranked BL>TD>OC in terms of competitive ability.

Study of TD→BL→OC and TD→OC→BL

When TD was the first species to be introduced, the percantage of TD parasitism as single-species parasitization as well as the superparasitism percentage were greater than when TD was introduced after BL or OC or both. This indicated that when there was no opportunity for TD to perform cleptoparasitic behavior, TD used superparasitism to avoid encapsulation. Therefore the HCE% in TD single-species parasitization cases was similar to some of the findings when TD was introduced as the second or third species (Table 53).

OC and BL's inability to discriminate interspecifically benefited TD, especially when those two species were released as the second species.

There was more BL/TD than OC/TD found in TD→BL→OC cases, and more OC/TD than BL/TD was found in TD→OC→BL (Table 53). These findings indicated that TD might have introduced a small amount of marking material into the hosts and because distribution progressed slowly, the third species introduced could have detected TD's presence better than the species introduced second.

Similar results were obtained from 75 observed multi-species interactions between TD→OC→BL (Table 54) and from 76 interactions between TD→BL→OC (Table 55). TD was a better intrinsic competitor than BL and OC. If these experiments had been carried out in an open area, for example in the field instead of in confined cages, the BL parasitoids' host discrimination ability would have allowed them to space themselves well over the area. As a result, there would have been little likelihood of multiparasitism. Consequently, the chance of TD escaping encapsulation would have declined.

When dissected and reared samples were compared, BL had the lowest parasitism in the TD→OC→BL dissected samples, and had the same as TD in the TD→BL→OC dissected samples. However, after the samples were reared BL had the highest percent parasitism since the percentage increased significantly (X^2=16.8 and X^2=5.28) (Table 42). This finding indicated BL was the superior of the three species. TD had the highest percent of parasitism in the dissected samples of TD→OC→BL and TD→BL→OC tests, and the next highest percentage of parasitism in reared samples. The percent of parasitism in reared TD samples was significanlty smaller than that found in dissected samples (X^2=22.63 and X^2=27.5). Of the three species, OC had the lowest percent of parasitism in the dissected samples of TD→OC→BL. OC was also the species with the lowest percent of

Table 53--Extended.

No. parasitized=303	3 spp.		27(7.3)	27(7.3)	27(7.3) (HCE(%)=2(7.4))	27(7.3)
% parasitism=81.5	2 spp.		46(12.4)	86(23.1)	86(23.1)	109(29.3)
	BL/OC	23(6.2)	23(6.2)			
	BL/TD	23(6.2)			23(6.2)	
	OC/TD		63(16.9))		63(16.9) (HCE(%)=12(11))	
	Total		108(29.4)	166(44.6)	192(51.6)	303(81.4)

* BL/OC = BL and OC multiparasitized the same host.
BL/TD = BL and TD multiparasitized the same host.
OC/TD = OC and TD multiparasitized the same host.

Table 54. The outcome of observed interactions when exposure sequence was TD→BL→OC.

Species combination	BL +	BL -*	OC +	OC -	TD +	TD -	Total
BL/OC/TD	11	10	4	17	17	4	21
BL/OC	4	1	0	5			5
OC /TD			4	14	14	4	18
BL/TD	8	14			14	8	22
Total	23	25	8	36	45	16	66
(+)%	48%		18%		74%		

*+ = "alive"; - = "killed."

Table 55. The outcome of observed interactions when exposure sequence was TD→OC→BL.

Species combination	BL +	BL -*	OC +	OC -	TD +	TD -	Total
BL/OC/TD	10	13	2	21	20	3	23
BL/OC	3	5	3	5			8
OC/TD			4	25	22	7	29
BL/TD	4	11			11	4	15
Total	17	29	9	51	53	14	75
(+)%	37%		15%		79%		

*+ = "alive"; - = "killed."

parasitism in the reared samples. That percent was significantly lower than the percent found in dissected samples ($X^2=29.86$). In TD→BL→OC tests, OC had the lowest percent of parasitism in both dissected and reared samples, with a significant decrease in the reared samples ($X^2=24.1\%$). However, compared to TD, OC showed a slightly smaller degree of decrease. Of the emerged parasitoids, less than 10% were OC (6.04%) and about 20% (18.4%) were TD. Thus, OC should have been considered inferior to TD. Therefore, order of comparative dominance within the larval guild as shown by both the TD→OC→BL and TD→BL→OC tests would be BL>TD>OC.

Study of DG as the Last Species Introduced in the Four-species Experiments

The results of the experiments in which DG is introduced 48 hours after the hosts were removed from the other three species are found in Table 56. In Chapter II it was noted that DG was the most efficient biocontrol agent in terms of intraspecific discrimination and oviposition restraint ability. These studies indicated a higher multiparasitism percentage (66.7% to 84%) compared to the superparasitism percentage (0 to 5.5%). As mentioned earlier, in the BL→DG, OC→DG, and TD→DG tests, approximately 40 hours lapsed between oviposition by the previous species and oviposition by DG. The internal markings made by the species previously exposed to the host probably disappeared when the host puparium was formed. Alternately, DG may have been unable to detect the internal marking substances because DG usually laid their eggs attached internally to the puparium and outside the true pupa. DG therefore did not penetrate the true pupa with their rather short ovipositors (0.25 cm).

Table 56. The results of interspecific competition when DG was introduced as the fourth species.

Sequential exposure	Total no.	No. singly parasitized (%)	No. super-parasitized (%)	No. multi-parasitized (%)	No. interspecific interactions in which DG was the superior (%)	Remarks
BL→OC→TD→DG	66	13(19.7)	3(4.5)	50(75.8)	48(96)	2 DG killed by BL
BL→TD→OC→DG	59	8(13.6)	3(5.1)	48(81.4)	48(100)	
OC→BL→TD→DG	50	8(16.0)	0(0.0)	42(84.0)	41(98)	1 DG killed by BL
OC→TD→BL→DG	60	17(28.3)	3(5.0)	40(66.7)	39(98)	1 DG killed by BL
TD→BL→OC→DG	79	19(24.0)	1(1.3)	59(74.7)	59(100)	
TD→OC→BL→DG	68	10(14.7)	2(2.9)	56(82.4)	56(100)	

Since DG defeated over 96% of the other three species when their interactions were observed, DG was considered superior to BL, OC, and TD (Table 56). When the parasitism percentages of each species in dissected samples were compared to the emerged parasitoids from reared samples (Table 42), DG was not always a more successful species than BL. In BL→OC→TD→DG, BL→TD→OC→DG, and OC→BL→TD→DG tests, both BL and DG did not show significant differences between the dissected and reared samples. However, BL was the species with the highest parasitism percentage in both samples. Therefore, compared to DG, BL was the superior extrinsic competitor in terms of searching for hosts. When BL was introduced as the third species (OC→TD→BL→DG, TD→OC→BL→DG) or introduced after TD (TD→BL→OC→DG) as a second species, DG became the superior species compared to the other species, including BL. This was because DG was the only species which demonstrated a significant increase in parasitism percentage in reared samples and at the same time the highest percentage of parasitism. In the BL→OC→TD→DG study, both OC and TD showed significant decreases in the percent of parasitism in reared samples. The decrease in OC was greater than in TD. In dissected and reared samples BL and DG showed no significant differences in the percent of parasitism. BL, however, demonstrated a higher percentage of parasitism in both samples than did DG. Therefore, order of dominance within the parasitoid guild would be BL >DG >TD >OC.

In BL→TD→OC→DG tests, TD and OC showed similar decreases in percent of parasitism in reared samples (X^2=25 vs. X^2=29.6). Also, TD and OC accounted for less than 10% of the emerged parasitoid population. They, therefore, had similar competitive abilities. Because the results for BL and DG in these BL→TD→OC→DG tests were similar to those found

in the BL→OC→TD→DG tests, order of dominance within the parasitoid guild would have been BL>DG>TD=OC. Using the same analysis system, the dominance in OC→BL→TD→DG would have been BL>DG>TD>OC, in OC→TD→BL→DG it would have been DG>BL>TD=OC, in TD>OC>BL>DG it would have been DG>BL>TD>OC, and in TD→BL→OC→DG it would have been DG>BL>TD>OC.

The study also examined the mortality inflicted by parasitoids and the percentage of hosts which successfully produced parasitoids. The total mortality of the hosts in multi-species groups was commonly higher than in single-species groups. However, the percent of parasitoids produced was not necessarily greater in the multi-species groups than in the single-species groups (Table 42). The total mortality and percent of parasitoids produced were relatively lower in the simultaneous exposure group than in the sequential exposure groups (Table 57). The pattern found here was similar to the one in the intraspecific competition studies (Chapter II). The greater the competition intensity, the greater the mortality and the more a male-dominated sex ratio could be expected. The competition intensity was greater in the simultaneous exposure group since both intraspecific and interspecific competition were involved, and thus a male-dominated sex ratio was found in this group (Table 57).

In the sequential exposure experiments, the pattern of sex ratio changes might have been influenced by the result of competition. The progeny of a superior competitor would tend to be female. In some cases, the sex ratio also was influenced by the order in which the parasitoids were exposed to the hosts. When BL was exposed first, the female-dominated sex ratio was comparable to the check group (σ:♀=1:2). When BL was introduced as the second or the third species, the female-dominated sex ratio was not as strong as when BL was first species

Table 57. The total mortality, percent of F_1 parasitoid emergence, and sex ratio results from simultaneous exposure experiments.

	BL		OC		TD		% F_1 Parasitoid emergence	Total mortality
	No.	♂:♀	No.	♂:♀	No.	♂:♀		
CK		1:2		1:2.4		1:1		
BL/OC/TD	297	1:1	34	1:0.8	76	1:0.7	14.6	74.2
BL/OC	247	1:1	90	1:2.3			16.4	59.3
BL/TD	156	1:1.3			163	1:0.6	15.3	53.3
OC/TD			66	1:0.7	117	1:0.3	11.8	57.9
1:$\bar{x}$ (±S.D.) ♂:♀	1:1.1(±0.2)		1:1.3(±0.9)		1:0.5(±0.2)			

(Table 58). The reduced number of female progeny might have been due to increased competition intensity, since the female may have laid more unfertilized eggs when it encountered more parasitized hosts. BL maintained a balanced sex ration (♂:♀=1:1.8) which remained close to the check group after various sequential exposure conditions (Table 58).

When OC and TD experienced interspecific competition, no identifiable pattern of changes in sex ratios developed. This may have been because the competition intensity varied with the conditions present at the moment and the competitive superiority of the two species changed in response to those conditions. Nevertheless, OC or TD were never superior to BL or DG in overall competitive ability. However, OC managed a female-dominated sex ratio in most conditions. Its average sex ratio (♂:♀ =1:2) was comparable to that of the check group (♂:♀=1:2.4). TD's average sex ratio (♂:♀=1:0.8) was also comparable to that of the check group (♂:♀=1:1), but under most conditions (11 out of 17) the sex ratio became more male-dominated. Therefore, in most cases interspecific competition altered the sex ratio of TD progeny in favor of males (Table 58).

DG was the only species whose sex ratio remained constant. In most cases the DG sex ratio was female-dominated (♂:♀=1:2) and was similar to that of the check group (♂:♀=1:2.3). This was because DG experienced only very limited competition. Because of its inability to discriminate interspecifically, DG was more frequently involved in interspecific competition than in intraspecific competition. However, DG's use of physiological suppression made it a superior intrinsic competitor in most interspecific cases.

Table 58. Progeny sex ratios of sequential exposure experiments.

Experiments	BL ♂:♀	OC ♂:♀	TD ♂:♀	DG ♂:♀
CK	1:2	1:2.4	1:1	1:2.3
BL→OC	1:1.9	1:0.5		
BL→TD	1:2.6		1:0.6	
BL→DG	1:2.2			1:2.3
OC→BL	1:1.7	1:0.7		
OC→TD		1:2.5	1:0.6	
OC→DG		1:5.6		1:1.5
TD→OC		1:1.3	1:0.8	
TD→BL	1:1.5		1:0.6	
TD→DG			1:1.2	1:2.3
BL→OC→TD	1:2.0	1:2.3	1:0.7	
BL→TD→OC	1:1.9	1:0.6	1:0.2	
OC→BL→TD	1:1.3	1:1.6	1:0.6	
OC→TD→BL	1:1.9	1:1.9	1:0.7	
TD→OC→BL	1:1.2	1:2.3	1:1.2	
TD→BL→OC	1:2.2	1:0.8	1:1.5	
BL→OC→TD→DG	1:2.2	1:4.0	1:1	1:3.1
BL→TD→OC→DG	1:2.2	1:2.0	1:0.5	1:0.8
OC→BL→TD→DG	1:1.8	1:1.6	1:0.4	1:2.4
OC→TD→BL→DG	1:1.5	1:1.9	1:1	1:1.5
TD→OC→BL→DG	1:1.1	1:1.5	1:0.6	1:2.2
TD→BL→OC→DG	1:1.1	1:3.2	1:1.2	1:1.9
$1:\bar{x}$ (±S.D.) ♂:♀	1:1.8(±0.4)	1:2.0(±1.3)	1:0.8(±0.3)	1:2.0(±0.7)

In general, the average sex ratio of progeny of each species through various conditions of interspecific competition was more or less similar to that of the check groups (Table 58). The similarity of the sex ratios to the check groups indicated that interspecific competition had less of an impact on sex ratio than intraspecific competition. Because of the latter, the sex ratios varied as the parasitoid-to-host ratios changed.

Multiparasitism and Encapsulation in TD

As observed in the vast majority of TD associated multiparasitism cases, little or no encapsulation was found. This interrelationship between multiparasitism and encapsulation should be emphasized.

TD was less encapsulated when multiparasitism was observed. The pooled data of the percentages of encapsulation of TD progeny (E%), and the percentage of TD parasitized hosts with all the TD progeny completely surrounded by hemocytes (HCE%) from all the TD associated parasitization was obtained from the sequential exposure experiments. The one exception was the TD/DG cases (Table 59). The E% was related to the survival of TD progeny inside the host. The HCE% was related to the portion of TD parasitized hosts which failed to produce any TD adults. There were significant differences of E% and HCE% between single-species parasitization (TD only) and multi-species parasitization (TD/BL, TD/OC, TD/BL/OC). However, there were differences between E% and HCE% when two or three species parasitized a host (t-test, Sokal and Rohlf 1969). In the TD-only group, about 90% of the TD progeny was encapsulated by hosts, and 3% (100-97.3=2.7%) of the TD parasitized hosts would have been able to successfully produce TD adults (Table 59). In contrast, less than 8% of the TD progeny were found encapsulated in two-species and three-species parasitized hosts (8.08% and 4.10%, respectively). The HCE% obtained

Table 59. Pooled data of E% and HCE% in different TD associated species cominbations.

Species Combination	No. TD parasitized hosts I	Total no. TD II	$\bar{X}$ (II/I)	No. TD encapsulated III	E% (III/II) x 100%	No. hosts with all TD progeny completely encapsulated IV	HCE% (IV/I) x 100%
TD only	338	939	2.78 a*	846	90.1 a	332	97.3 a
TD/BL, TD/OC	554	1163	2.10 a	94	8.08 b	73	13.2 b
TD/BL/OC	113	268	2.37 a	11	4.10 b	8	7.0 b

*Values followed by the same letter in the same column mean no significant difference by t-test, p=0.05.

when two species parasitized the host was 87% (100-13.2=86.8%). When three-species parasitism was used, the HCE% was 93% (100-7=93%) (Table 59).

Superparasitism was also used to avoid encapsulation; however, multiparasitism results in fewer eggs wasted, a lower E% and a lower HCE% than superparasitism (Tables 8 and 59). Therefore, multiparasitism is a more efficient way for TD to avoid encapsulation.

The encapsulation-inhibitory factor could have been from the eggs or larvae of OC or BL. This was suggested in the case of P. bochei parasitizing D. melanogaster where P. bochei progeny provided protection to P. mellipes (Walker 1959, Streams and Greenberg 1969). Alternately, the OC or BL females may have released a toxic substance during oviposition. This phenomenon was observed by Pemberton and Willard (1918) when toxic substances produced by females of the braconid O. fletcheri prevented the host D. cucurbitae from encapsulating the chalcid T. giffardianus. In some cases, although TD was introduced before BL or OC, TD was still protected since it experienced little or no encapsulation. Apparently, the host was unable to mobilize its defense mechanism before the anti-encapsulation substance was released. Further study regarding this would be of value.

As observed in the preceeding sequential exposure studies, TD behaved cleptoparasitically and favored the multiparasitization of its host, but it did not always kill the previous primary species. Thus, this cleptoparasitic species does not meet the definition of a cleptoparasitoid developed by Spradbery (1968) in which the cleptoparasitic species is expected to kill the previous species. Although multiparasitism affords

TD a higher probability of survival, the species cleptoparasitic behavior has not evolved to the point of fully meeting the criteria of a clepto-parasitic species.

CHAPTER VI
GENERAL DISCUSSION AND CONCLUSIONS

In order to obtain an overall evaluation of these four interacting species, a ranking system was devised. In this ranking system, '1' was most desirable in terms of inflecting host mortality; '4' was the least desirable. The species' biological characteristics, reproductive capacity, and competitive ability were evaluated. To determine the overall ranking, it was necessary to determine the species' score on each of these.

The ranking system of some basic biological characteristics is presented in Table 60. BL had the longest ovipositor (0.55 cm) thus it was able to detect deeply concealed hosts and avoid exploiting the same hosts as OC and TD. The lengths of OC and TD's ovipositors were 0.30 cm and 0.25 cm, respectively. The length of DG's ovipositor (0.25 cm) was comparable to TD's, but DG used a different ecological niche (pupa) from that used by TD or OC (larva). DG females had a greater longevity (30-37 days) than BL (14-20 days), OC (10-15 days), or TD (15-18 days). The DG female therefore had the advantage of an extended searching period. Encapsulation was only observed in TD parasitized hosts. It resulted in a wastage of TD progeny, time, and hosts. Encapsulation indicates that TD lacks a mechanism to overcome host defense and therefore is the least desirable species as a control candidate. All four studied species exhibited host discrimination behavior. The egg distribution analysis showed OC deposited its eggs in a random distribution and TD demonstrated

Table 60. Ranking of BL, OC, TD, and DG on basis of specific biological characteristics.

Characteristics	Rank of species			
	BL	OC	TD	DG
Ovipositor length	1.5	3.5	3.5	1.5
Female longevity	2.5	4	2.5	1
Host-defense mechanism	2	2	4	2
Superparasitism	2.5	2.5	4	1
Sum of rank	8.5	12	14	5.5
Overall rank	2	3	4	1

a tendency to superparasitize hosts. DG showed better oviposition restraint than the other three species when the parasitoid-to-host ratio was high. Superparasitism was found in all four species. DG had the smallest percentage of superparasitism (3.2%), and the smallest average number of eggs per parasitized host (2.17). BL and OC demonstrated similar degrees of superparasitism (21.1% in BL, 15.2% in OC) as well as a similar number of eggs per parasitized host (2.46 vs. 2.71). TD had the highest degree of superparasitism (52.5%) and the highest average number of eggs per parasitized host (3.27). The overall evaluation of the biological characteristics of these four species resulted in the following ranking: DG>BL>OC>TD. TD was thus the weakest candidate for a biological control program.

To rank the parasitoids on competitive ability, two types of experiments were used: DG involved experiments, and non-DG involved experiments. When DG was not involved, the ranking of the competitive ability of the three larval species was BL>TD>OC (Table 61). When DG was involved, the parasitoid ranking was DG=BL>TD>OC (Table 62). Since the DG involvement did not change in the larval species ranking, the overall ranking of competitive ability was DG=BL>TD>OC.

The ranking of reproductive capacity is presented in Table 63. TD was the most desirable species since it demonstrated the highest biotic potential (146.8 eggs/ovary) and the highest per female fecundity (55.7 eggs/day). BL's biotic potential was 47.4 eggs/ovary and its female fecundity was 30.7 eggs/day. OC's biotic potential was 39.8 eggs/ovary and female fecundity of 25.7 eggs/day. DG was the least desirable species as it has the smallest biotic potential (3.06 eggs/ovary) and the

Table 61. Ranking of larval parasitoids (BL, OC, TD) on basis of competitive ability.

Exposure experiments	Rank of species		
	BL	OC	TD
Simultaneous exposure			
BL/OC	1.5	1.5	
OC/TD		2	1
TD/BL	1.5		1.5
BL/TD/OC	1	3	2
Sum of rank	4.0	6.5	4.5
Sub-overall rank	1.5*	3	1.5*
Sequential exposure 2-species			
BL→OC	1	2	
OC→BL	1	2	
BL→TD	1		2
TD→BL	1.5		1.5
TD→OC		2	1
OC→TD		2	1
Sum of rank	4.5	8	5.5
Sub-overall rank	1	3	2
3-species			
BL→OC→TD	1	3	2
BL→TD→OC	1	2.5	2.5
OC→BL→TD	1	3	2
OC→TD→BL	1	3	2

Table 61--Continued.

Exposure experiments	Rank of species		
	BL	OC	TD
3-species (cont.)			
TD→BL→OC	1	3	2
TD→OC→BL	1	3	2
Sum of rank	6	17.5	12.5
Sub-overall rank	1	3	2
Sum of sub-overall rank	3.5	9	5.5
Overall rank	1	3	2

*The difference of sum of rank between BL and TD is less than one gradation unit (1); therefore, BL and TD share the same rank in sub-overall rank.

Table 62. Ranking of BL, OC, TD, and DG on basis of competitive ability.

Sequential exposure	Rank of species			
	BL	OC	TD	DG
2-species				
BL → DG	2			1
OC → DG		2		1
TD → DG			2	1
Sum of rank	2	2	2	3
$\bar{X}$ rank	2	2	2	1
Sub-overall rank	2	2	2	1
4-species				
BL → OC → TD → DG	1	3.5	3.5	2
BL → TD → OC → DG	1	3.5	3.5	2
OC → BL → TD → DG	1	4	3	2
OC → TD → BL → DG	1	3.5	3.5	2
TD → OC → BL → DG	2	4	3	1
TD → BL → OC → DG	2	4	3	1
Sum of rank	8	22.5	19.5	10
Sub-overall rank	1	4	3	2
Sum of sub-overall rank	3	6	5	3
Overall rank	1.5	4	3	1.5

Table 63. Ranking of BL, OC, TD, and DG on basis of reproductive ability.

Characteristics	Rank of species			
	BL	OC	TD	DG
No. eggs/ovary	2	3	1	4
No. eggs/female/day	2	3	1	4
Sum of rank	4	6	2	8
Overall rank	2	3	1	4

Table 64. Overall ranking of BL, OC, TD, and DG on basis of various qualities.

Characteristics	Rank of species			
	BL	OC	TD	DG
Reproductive capacity	2	3	1	4
Biological characterists	2	3	4	1
Competitive ability	1.5	4	3	1.5
Sum of rank	5.5	10	8	6.5
Overall rank	1	4	3	2

smallest female fecundity (4.9 eggs/day). Thus, the overall ranking of reproductive ability was TD>BL>OC>DG.

The overall evaluation of these interacting species based on biological, reproductive, and competitive ability was BL>DG>TD>OC (Table 64). These findings represent an exception to the r-K continuum guild system. The BL parasitoid demonstrated a high reproductive capacity as a r-strategist, and a superior competitive ability as a K-strategist. Thus, BL met more of DeBach's "best" parasitoid criteria than the other three species (DeBach 1974). Nevertheless, according to the r-K continuum guild system, DG performed as a typical K-strategist with its low reproductive capacity and superior competitive ability.

TD acted as a cleptoparasitoid. This behavior contradicted the generally held view that cleptoparasitism is no more than a lazy parasitoid's method of finding a host. Instead, it was selectively advantageous to the TD parasitoids and used as a survival strategy. In biocontrol programs, cleptoparasitoids are treated as hyperparasitoids and are excluded from importation. The exclusion of hyperparasitoids and cleptoparasitoids from biocontrol programs is based on the belief that such introduction may seriously impair the primary parasitoid's ability to control its host. While some believe that hyperparasitism and/or cleptoparasitism under certain conditions may act as a stablizing factor (Luck and Messanger 1967, Luck et al. 1981), far too little is known about these conditions to justify the introduction of hyperparasititoids or cleptoparasitoids for biocontrol purposes. In this study, the cleptoparasitic behavior of TD interfered with the control efforts of BL. As a result, the number of BL parasitoids was reduced in tests where

these two species were in competition. When fewer BL-parasitized hosts were available, TD superparasitized healthy hosts. Eggs and energy were therefore wasted and fewer hosts were parasitized. Therefore, based on this study, TD is not recommended for release.

For a biocontrol program to be successful, it is not only imperative to suppress the pest insects, but also it is necessary to produce adequate parasitoid progeny to assure the survival of the F_2 parasitoid generation. The host mortality caused by OC acting alone--or by OC acting in conjunction with another of the three species--was comparable to the host mortality obtained by using other combinations of species (Table 42). However, OC always produced fewer progeny than BL or DG (Table 42). Ring-structure damage was also a major mortality factor attributed to OC. This damage was a type of predaceous behavior in which OC killed the host without laying any eggs. Because ring-structure damage would suppress the host population, OC would be a helpful control agent only if it were used with BL in situations where the host density was high. OC's inferior competitive ability and tendency to cause unnecessary ring-structure damage would be serious liabilities when the host densities were low. In those circumstances, OC would become scarce in the field. Thus, OC would be an appropriate choice for a release program only if BL and DG were unavailable.

DG oviposited in puparia and developed ectoparasitically on pupae, a different ecological niche from the other three species. Although it demonstrated a rather low reproductive capacity, DG had a relatively long life span and was a superior competitor. It was a typical K-strategist, and operated well at low host densities. When this species, accompanied by BL was released, host mortality was 80%, and adult emergence was 33%

(Table 42). This was comparable to the multispecies release tests involving three or four species (Table 42). The study of interspecific competition indicates that release of BL and DG together was definitely more effective in reducing the host population than the release of BL or DG alone. Based on this information, DG would be expected to complement the control efforts of the BL parasitoids already established in the field. Therefore, DG is recommended for release as a biological control of A. suspensa. Initially, in attempts to establish a field colony, a small number of DG should be released at any given site to augment the female-dominated population of F_1, because the limited competition and contamination in the area would then favor female progeny production.

The present findings confirm the importance of becoming familiar with the biology of each species and the interactions within or among species prior to introducing the parasitoids into the fied. An example of this is cleptoparasitic behavior, which is presumed to be detrimental to biocontrol but which would not be detected without the careful study of interspecific interactions.

Because the study of biologically specific characteristics and laboratory analyses cannot be used as a completely accurate reflection of field conditions, field experimentation is recommended. Ideally, these field experiments would provide information about whether parasitoid competition plays a key role in population dynamics, and whether other factors, such as pathogens or weather, influence the effectiveness of the control agent.

Further research would enhance the understanding of the encapsulation mechanism. In turn, this would broaden our comprehension of the physiology of endoparasitic Hymenoptera. Therefore, it would be helpful

to study the timing of encapsulation of TD eggs as well as the timing and nature of substances released by the other species that serves to neutralize the host's defense mechanism.

Because the ring-like structure due to OC, as well as encapsulation of TD was found in the non-native host, A. suspensa, further studies of the nature of the ring-like structure and encapsulation are recommended. These studies will lead to the understanding of the beginning of the co-evolution of any new host-parasitoid relationship.

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BIOGRAPHICAL SKETCH

An-ly Yao was born on November 23, 1948, to Mr. and Mrs. S.C. Yao in Taipei, Taiwan, R.O.C. She received her B.S. in entomology from National Chung-tsing University, Tai-chung, Taiwan, in 1971. She was employed by the Citrus Research and Development Center, Tsin-chu, Taiwan, as a research assistant from July, 1971, to January, 1973. While there, she developed a mass rearing program for the oriental fruit fly Dacus dorsalis Hendel. In August, 1973, she received a scholarship from the Food Institute, East-west Center, to study for a master's degree in entomology at the University of Hawaii under Dr. T. Nishida. After completing her master's degree in October, 1975, she was employed as an assistant researcher by the Insect Ecology Laboratory, Institute of Zoology, Academia Sinica, Taipei, Taiwan, R.O.C. There she worked on sterile insect techniques and a population survey of D. dorsalis. An-ly was admitted as a Ph.D. program student in the Department of Entomology and Nematology, Unviersity of Florida, in September, 1979. Upon completion of her Ph.D. degree, An-ly will join the Insect Ecology Laboratory, Institute of Zoology, Academia Sinica, Taipei, Taiwan, R.O.C., as an associate researcher.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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